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# THE INCREASE OF THE BADGER (*MELES MELES*) IN GREAT BRITAIN DURING THE PERIOD 1900–1934:

## WITH ESPECIAL REFERENCE TO AN AREA IN SOUTH SHROPSHIRE KNOWN AS THE WHEATLAND COUNTRY

BY FRANCES PITT.

(*With Plate* 1 *and* 2 *Maps in the Text.*)

THE increase in the numbers of the badger (*Meles meles* Linn.) in many parts of Great Britain during the past thirty years has been marked. Formerly comparatively scarce, it has risen to be one of the more plentiful of our larger mammals. Owing, however, to its nocturnal habits it is not a noticeable mammal and may be overlooked; nevertheless its numbers and distribution in any given area can be ascertained with fair accuracy because its large burrows ("earths" or "sets") are easily discovered.

These burrows are usually of considerable size, with far-reaching tunnels, the excavated earth being witness to the industry of the inhabitants. Very big sets may be occupied by two, three or possibly more pairs of badgers, but the less extensive ones may be inhabited by only a badger or two. Throughout this paper "pairs" of badgers are referred to, but this is merely in description of couples of breeding animals, and is not intended to carry the meaning that the badger pairs after the manner of the fox. The writer believes it does, possibly pairing for life, but proof is lacking.

Badgers will sometimes, and for no apparent reason, leave an earth for a while, but they usually return to it. Unless the badgers of a particular earth are exterminated by keepers, that burrow will be occupied off and on for many generations. Even when the animals are much persecuted and their set repeatedly dug out they seem loath to leave home. I only know of two earths being abandoned.

Such disputed questions as the mating time of the badger and its period of gestation do not concern us here when dealing with its increase, but the fact that it has a small litter, generally of no more than two, three or four cubs, born between the beginning of February and the end of March, has bearing on the matter. It is open to question if every couple has young every spring, also if the female breeds in her first season, these questions being raised by non-breeding animals found in the spring and the many earths that fail to show signs of litters.

Certainly the badger has a low rate of increase. But it is probably a fairly long-lived animal. Captive badgers two or three years of age show no sign of

their teeth wearing, and of wild killed badgers I have handled the same may be said, with a single exception. This was a large male badger found dead,

Map. 1. Distribution of the badger in 1900 in that part of South Shropshire known as the Wheatland country. Each dot represents one pair of badgers. (Based upon the Ordnance Survey Map, with the sanction of the Controller of H.M. Stationery Office.)

lying curled up in a natural position beneath a thick rhododendron bush, near a large well-used badger earth. He appeared to have died of senile decay. His teeth were worn right down and he showed signs of extreme old age.

So far as I am aware the adult badger has no enemies in Britain save man. Cubs may now and again be killed by a jealous fox (vixen with cubs) in the absence of their dam. As for disease, I have never seen an unhealthy wild badger, old or young, though a tame badger belonging to a friend died at twelve months old with an inflamed throat. As members of the Mustelidae do suffer from these throats (I have lost a pet otter and many ferrets from them), which Prof. Sir Frederick Hobday tells me may be a form of acute tonsillitis, it is possible we here have a factor that keeps down the numbers of the badgers. This, however, is mere surmise.

Having considered how few factors there are to militate against the badger, let us consider its increase in a particular area, namely that piece of country in Shropshire which lies between the river Severn on the east, the Clee Hills on the south-west, and on the north is bounded by a line running roughly from the verge of the Church Stretton hills to the Severn at Buildwas. The eastern side of this triangle is about 17 miles in length, likewise the south-west, while its width at the northern end is about 12 miles (85·6 sq. miles).

The district is an undulating, well-watered one, with many and extensive woodlands. The soil varies from that of a light sandy nature near Bridgnorth (red sandstone), and the heavy wet clays of the central district, to the limestone of Wenlock Edge; but details of the soils and situations are given under individual headings in the list of earths below.

*Badger earths in the Wheatland country, the estimated inhabitants being indicated by a dot per pair before the number of the set.*

● 1. Plaish Dingle. This earth is in two sections about 30 yd. apart and has been used the past nine or ten years. It has often been occupied by a number of badgers. Limestone.

●● 2. Preen Manor. I first discovered badgers here in the winter 1930–1, occupying tunnels between limestone slabs; later they invaded a culvert in the garden; both places amid bushes and trees. Limestone.

● 3. Harley Bank, in Wenlock Edge, an old earth in the Edge Wood, probably been there fifteen to twenty years. Has been attacked by badger diggers and twice in an endeavour to get out foxes. Limestone.

●●● 4. Tickwood, north side, an ancient stronghold in a big woodland occupied by many badgers. Limestone.

● 5. Spratts Coppice, an artificial fox-earth continually used by the Tickwood overflow badgers. Limestone.

●● 6, 6 A, and 6 B. Caughley, large woodland, heavy clay soil, with sandy pockets in which the badgers dig. Always badgers here, though persecuted by the keepers, earths 6 A and 6 B were trapped until the animals abandoned them and are not in use now.

● 7. Tarbatch Dingle, big earth, perhaps twenty years old, in wooded valley. Clay, but earth in dry bank.

● 8. The Albynes, an artificial fox earth put in 30 years ago, was annexed at once by badgers, enlarged and made into a set and has been occupied off and on ever since. Woodland, heavy clay.

● 9. Shirlett. Large woodlands. Big earth in clay.

◗ 10. Wilderley. One badger has haunted this wood for three years, lodging sometimes in an artificial fox-earth and when ejected in an enlarged rabbit-hole. This wood is very wet. Clay.

● 11. Deepdale, Stanley. Sandy woodland. Large colony, ten to fifteen years old.

●● 12. Ferny Bank, Stanley. Sandy rough bank, trees and bushes. Very strong colony, several burrows, about nine years old.

●● 13. The Hurst, Aldenham. A big earth in a bushy quarry (gravelly soil) begun nine years ago.

● 14. Spoonhill. Large wood, clay land, big badger earth.
● 15. Caulleys. Badgers continually use the artificial fox-earth. (Clay, but earth in dry bank.)
●● 16. The Moor House Dingle, Larden; an enormous badger warren in a sandy-banked dingle, perhaps dating back eight years.
●● 17. Stanway Bank, ferny limestone bank, a very old stronghold.
● 18. Roman Bank, Stanway, in a wood, on limestone bank, another old earth.
●●● 19. Little Oxenbold Wood, this is a recent excavation, begun about five years since, in a gravelly pocket in clay surroundings. It is a huge warren.
●● 20, 20 A. Monkhopton, one earth on dry bank, the other in a wooded dingle. The first is a very old earth. Clay, but earths in dry banks.
● 21. Netchwood. A badger or two usually in residence in the dingle. Clay.
● 22. Hare's Parlor, well-used earth, dug about seven years back. Clay.
●● 23. Yew Tree Dingle, Meadowley, a big place, well used for the last nine years. Clay.
● 24. Hell Hole, Meadowley. Medium earth. Clay.
●● 25. Fox-holes, Thatcher's Wood, an ancient stronghold, the tunnels running beneath shelves of rock.
● 26. Minchuels Dingle, a sandy hole between rock shelves.
◗ 27. Lodge Coppice, a single badger has patrolled this wood for the past two years.
● 28. The Clee Hill, badgers here much persecuted by the keepers, but a pair or more hold out, first in one place, then in another.
●●● 29. Sidbury. This is a new earth, begun two years ago, and is now enormous. It is on an open bank, which consists of sand and gravel. The surrounding land is heavy and wet.
● 30. Chelmarsh Bottoms. An old place. (Clay, but earth in dry bank.)
● 31. The Riddings Dingle. A big earth in gravelly soil.
● 32. The Crunnels, an old earth in gravelly land.
● 33. The Deserts, a hole dug in an old charcoal burning.
● 34. Hampton Lode rocks. Wooded rocky slopes where foxes and badgers go to ground.
● 35. Stapley Dingle, an old earth between shelves of rock on a clay bank.
● 36. The Bylet, recently dug holes in clay. First signs of badgers here observed in 1930.

Except Nos. 20 and 29, all these sets are in woods or under trees, and all are within easy reach of water. Earths in the heavy clay land rarely occur in the clay (one does at Wilderley, 10), but are made in dry banks, in sandy or shaly layers between strata of clay, or (Monkhopton, 20 A) beneath shelves of rock.

The two maps show first the occupied badger earths during the winter 1933–4, thirty-seven in number, used, it is estimated, by fifty couples of badgers, or one hundred individuals; and secondly the few earths in existence in 1900, some ten with a population of about twenty-four badgers. The first is from personal inspection, but the second is from "hearsay" though of the most reliable description. The contrast is great. The probable error is in over-estimating the number of badgers thirty-four years ago and under-estimating them now. The basis on which it is assumed a pair of badgers occupy an earth is the amount of winter usage shown by the holes. Where an earth shows a good deal of traffic in mid-winter and footprints differing in size are found it is assumed that at least two badgers are present. Where the earth is very big and the usage yet more pronounced two couples are assumed. Spring and summer usage, when cubs make much mark, is not regarded. Corroboration of these estimates has been obtained when digging for foxes in winter and in one case by nightly observations at an earth in summer.

Access to woods, and earths in them, and frequent inspection of the earths, has been facilitated by my connection with the pack of foxhounds that hunt the district, namely the Wheatland, of which I am Master.

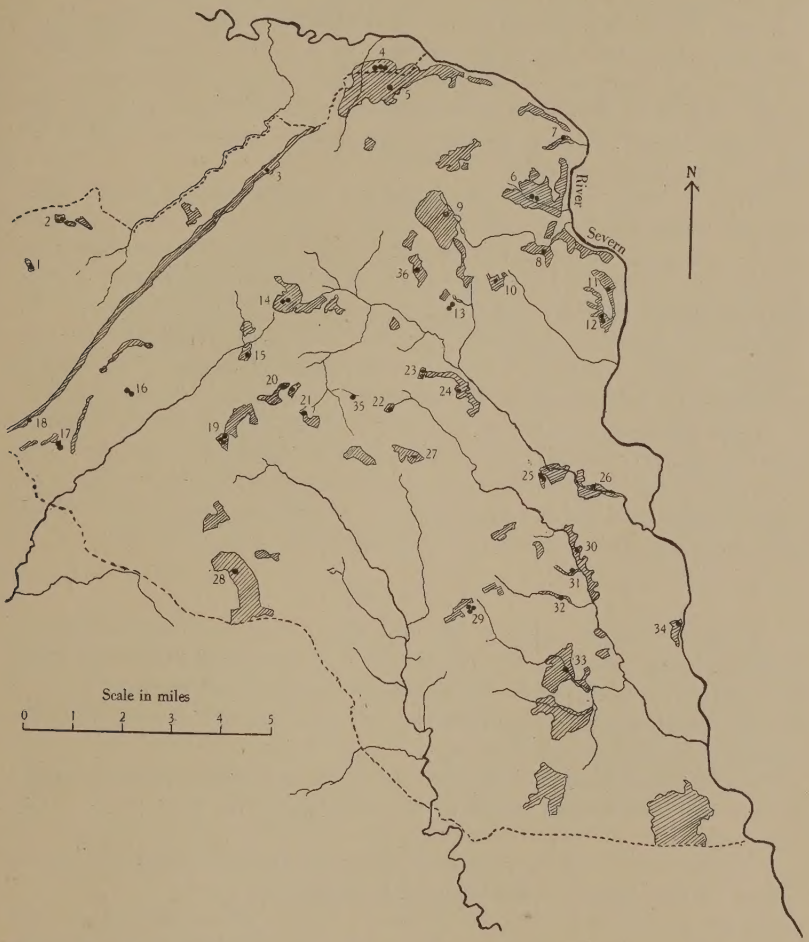
*Photo. Frances Pitt*

Phot. 1. Flashlight photograph of an old badger and young one coming from earth at night. Cub about half grown.

*Photo. Frances Pitt*

Phot. 2. A badger's "set" at the Albynes showing a quantity of discarded bedding.

This increase of badgers is not peculiar to the small district under consideration, but has been going on from the south of England to Scotland, where




Map. 2. Distribution of the badger in that part of South Shropshire known as the Wheatland country during the winter of 1933–4. Each dot represents one pair of badgers. Based upon the Ordnance Survey Map, with the sanction of the Controller of H.M. Stationery Office.

badgers are now found in districts where they were previously unknown. The multiplication of the badger in the wooded districts of the Welsh Border has been amazing. I attribute its increase, which became marked after the War, to the withdrawal of gamekeepers during the War, to the decrease of game

preservation and the present fewness of full-time gamekeepers. In the Wheatland district the keeper and the rabbit-catcher are the chief foes of this animal. Badger digging as a sport takes place too rarely to be considered as a factor in this area. Evidence *re* general increase of the badger in England, Scotland and Wales is derived from naturalist correspondents, sporting friends and gamekeepers, from comments in sporting journals, and from the annual returns made by Masters of Hounds to the journal *Horse and Hound* in which they give their "bags". Badgers now figure frequently in these returns, which are made by practically all packs.

When sparsely distributed the badger is a harmless and inoffensive mammal. The worst that can be said of it is that it digs up nests of young rabbits in the spring and takes rabbits from the rabbit-catchers' snares during the autumn and winter. In my experience stories of it raiding poultry houses, slaughtering young lambs and killing game are usually due to confusion with the deeds of foxes and wandering dogs; but "criminal" individuals do occur now and again, and it is possible, if the badger increases still further in numbers, such individuals, under necessity to find food, may likewise increase.

If its multiplication goes on, the badger may change its feeding habits to some extent, and possibly be transformed from a species that interferes little with man to one that is somewhat of a nuisance. It will be interesting to see what population of badgers a given piece of country can support, and whether the badger's progress will be eventually checked by disease—or man.

## 1. Summary.

1. All the badger earths in the Wheatland country of South Shropshire (85·6 sq. miles) were mapped in 1933–4. It was estimated that there were thirty-seven occupied earths containing at least one hundred animals.

2. Enquiries gave a rough estimate of ten occupied earths in 1900, containing some twenty-four animals.

3. This great increase during the last 33 years is believed to be part of a general increase common to many parts of Great Britain, of which the causes are discussed.

4. Further increase may cause the badger to become a pest, although at present it does only occasional damage to poultry.

# THE RANGE OF THE SEA-URCHIN *ECHINUS ESCULENTUS*

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(*With* 1 *Map in the Text.*)

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## 1. History.

In 1922 Miss E. Trewavas (**1**) recorded the occurrence of the sea-urchin, *Echinus esculentus* L., between tide-marks at Mousehole in Cornwall, and commented on the fact that it did not seem to be known from any other adjacent part of the coast. She noted that such specimens as she picked up were of large size, but she offered no suggestions as to the reason for such a local occurrence. Prof. J. H. Orton (**2**) later on noted the occurrence of the urchin between tide-marks at five different localities in the British Isles, viz. Mousehole, Whitby, Isle of Man, Millport and Kyle Akin, Skye. He accounts for the presence of the urchin above low-water mark, ordinary spring tides, by suggesting that, during the annual shoreward migration for spawning (**3**) those which arrive in a locality where low water (spring tides) does not fall in the hottest part of the day nor the coolest part of the night may appear above low-water mark, whereas those in other localities will be kept below that point by the danger of desiccation. He also points out that the spawning ground must have (1) a temperature (or correlated factors) greater than that of the deeper off-shore water, (2) a suitable rocky ground protected from excessive wave action, (3) an approach to the shore from off-shore without an intervening belt of fine sand.

Arising from Orton's paper, Hentschel (**4**) and Reid (**5**) added to the localities where the urchin was found above low-tide mark, the latter pointing out that on the north coast of Scotland the animal was found where low water (spring tides) fell in the hottest part of the day.

### 2. General distribution.

In order to deal adequately with the problem of the vertical range of *Echinus esculentus* it was considered advisable to examine its entire range. Since it has been found in the European seas from North Norway to Portugal, including the Kattegat, it may be safely called an Atlantic-European species. Its westward range carries it towards the Greenland coast, but it does not appear to reach the American continent. It does not occur south of Portugal nor in the Mediterranean. Although there is some doubt of its having been found in Spitsbergen (**6**), it is found as an in-shore species in the Lofoten Islands (**7**), Hardanger, Selbo, Kors, Bjørn, Bergens, Herlø, Hjelte, Manger, Sogne and Sond fjords (**8**). Indeed, to quote Döderlein (**6**): "The *Echinus* is spread along the whole coast of Norway, from Finmark to Skagerak and in Kattegat; in the North Sea to the Faroes."

On the German coast *Echinus* does not occur but is found on the banks, and this is probably true of the Dutch and Belgian coasts. J. le Gall (**9**) informs me that this species does not occur in the littoral zone of Pas de Calais, nor of Ostend. It is very rare in hauls from the open sea in that region, having been taken but once. It is not recorded in the "Fauna de Normandie". On the other hand from Finistère (France) southward it is very common in the sea (Legendre (**10**)) but does not become a littoral species until the Bay of Bidassoa is reached. There, and along the neighbouring coast of Spain, it is found in the intertidal region throughout the year (**11**). In Portuguese waters the urchin is very plentiful and is used for food in various places. It normally ranges from 10 fathoms (20 m.) downwards, but one specimen has been taken from the intertidal zone near Leixões and lived for two months in the aquarium at the marine station (**12**). The species occurs almost all round the British Islands, the Faroes and Iceland.

Its depth range lies between 0 and 1264 m. (**13**).

### 3. Intertidal distribution.

As has been seen, *E. esculentus* is found between tide-marks in Mousehole, Cornwall and in several other widely separated localities. A more extended survey has proved the animal to be much more common between tide-marks than was supposed (see Table 1). Unfortunately there is a want of accuracy in faunal lists which makes many records well-nigh valueless when everything depends upon precision of statement. To record an organism thus: "Common at *X* Point", is merely waste of good paper. This is the more irritating when an organism with an extended range is being referred to.

Table 1. *Habitats of* Echinus esculentus *in the British Isles.*

| Locality | Material of shore | Nature of weathered rock surface | Amount of wave action | Low water (spring tides) hours | Sea temp. (Aug.) ° C. | Source |
|---|---|---|---|---|---|---|
| | | | Shetland. | | | |
| Tressa Wick | Metamorphic | Fairly rough | "Sheltered" | 03.15 | 12–13 | See Hentschel |
| | | | North coast. | | | |
| Rispond (Loch Eireboll) | Gneiss | Smooth | Not great where E. occurs | 03.15 | 12–13 | D. M. R. |
| | | | West coast. | | | |
| Loch Inchard | Gneiss | Smooth | Slight | 02.16 | 12–13 | D. M. R. |
| Loch Laxford | „ | „ | „ | 02.16 | 12–13 | D. M. R. |
| Kyle Akin | Gneiss and schist | „ | „ | 01.13 | 12–13 | Orton (**2**) |
| Loch Sunart | Schistose and gneiss | „ | „ | 00.12 | 12–13 | D. M. R. |
| Clyde Area | Various | „ | „ | 07.19 | 12–13 | "Fauna of Clyde Sea Area" |
| Port Erin | On rough concrete blocks and smooth rocks near Breakwater | | | 06.18 | 13–15 | Orton (**2**) |
| Hilbre Island | — | — | — | 06.18 | 14–15 | 1 specimen caught in 1885; "Fauna Liverpool Bay" |
| | | | South coast. | | | |
| Mousehole | Granite | Smooth | Slight | 01.13 | 15–16 | Orton (**2**) |
| | | | East coast. | | | |
| St Andrew's | Sandy shales | — | — | 09.21 | 13–14 | Rare "Marine Fauna of St Andrew's" |
| Cullercoats | Sandstone | Smooth | — | 11.23 | 13–14 | Orton (**2**) |
| Robin Hood's Bay | Clay and shales | Smooth | — | 11.23 | 13–14 | Bromehead (**15**) |

It has not been possible to learn definitely where the urchin is found as an intertidal species on the Norwegian coast. Murray and Hjort (**14**) say in a general way that it is "common in the littoral zone among the skerries on the west coast of Norway". Other writers are not so precise. Grieg (**8***a*) records it from Hardanger Fjord, mostly on the outer coast, very common in "streamy water". This may mean tide-race, so it is likely that the specimens were in shallow enough water to be seen from the surface, hence they might have been on *Laminaria*. The Finmark record of 0·55 m. brings the *Echinus* into the intertidal fauna group. On the British coasts the urchin is comparatively abundant between tide-marks in suitable localities. The suitability factor will be discussed later.

There are but scanty records of this species as a littoral form on the Irish coasts. As has already been mentioned, it is common between tide-marks in the Bay of Bidassoa in south-west France and along the north coast of Spain, fading out with one recorded occurrence at Leixões on the Portuguese coast.

### 4. Factors likely to affect the vertical distribution.

#### (*a*) *The shore.*

Before anything can be said regarding the occurrence of *E. esculentus* on the shore it is necessary to develop a convenient classification of shore-forming materials. Although shores may be formed of as many diverse materials as there are minerals in the earth's crust, it would appear, from their physical nature at least, that they may be placed in one of two groups forming:

(1) The *Incoherent-littoral* composed of silt, mud, sand, shingle and boulders.
(2) The *Coherent-littoral* which can be subdivided into:
   (*a*) the *Coherent-smooth littoral* composed of such rocks as granite, gneiss, basalt, etc., which are worn smooth by the action of the sea and are of great permanence.
   (*b*) the *Coherent-rough littoral* composed of friable, fissile and easily eroded rocks which weather rapidly (e.g. many sandstones, limestones, shales, etc.) and, if not horizontally bedded, give rise to a very jagged type of shore.

If, however, any rocks of type 2 are horizontally bedded at such a height that they are subjected to wave action they offer no foothold for animal life. On type 1 *E. esculentus* does not occur, nor is it to be expected, since this type of shore is very unsuitable to the locomotor apparatus of the organism. Type 2*b* would, owing to its very uneven jagged surface, present few more advantages for echinoid locomotion than the previous type. On this type of rock *Echinus* is known to occur (at Robin Hood's Bay) (**15**) but it is comparatively rare. The bulk, one might almost say all, of the occurrences are on type 2*a*, where the smoother surfaces are best suited to the mode of progression of such an inflexible object as *Echinus*.

#### (*b*) *The slope of the shore.*

On this aspect of the case I have but little general data. At those places where I have myself found the urchin above low-water mark the steepness of the shore has always been very great. Indeed, I do not think it inexact to say that where specimens have been seen with greatest constancy the shore is vertical or nearly so. The steepness of the shore, therefore, would appear to be a considerable factor in deciding the presence or absence of *Echinus* above low-water mark.

The reasons for this are probably (1) the absence of tidal rush, so that the chances of the organism being "rolled" are reduced to a minimum. It should be noted, however, that once it has a firm hold with its tube-feet considerable force is required to displace *Echinus*. On rock at various angles (under water) tests were carried out on specimens of different sizes. A loop of string was passed round the shell. The free-end of the string was attached to a spring

balance which was raised until the urchin was drawn free. A force equal to from 4 to 6 lb. had to be exerted to dislodge the specimens.

(2) The tidal time distance factor. In the case of a vertical shore this would allow the maximum duration of rise and fall of the tide through the minimum distance and thus there would be less chance of a slow-moving form being left behind by the retreating tide, as would happen on a gently sloping shore.

### (c) *Amount of wave action.*

It will be noticed in Table 1 that where *Echinus* occurs the amount of wave-action is very slight. There is nothing particularly striking in this, for it is only what is to be expected, not only because of its physical effect on the organism but because, under such circumstances, there would be little or no vegetation. Since *E. esculentus* is largely a vegetable feeder it would not tend to move into barren areas.

### (d) *The nature of the foreshore.*

Orton (2) lays stress on the nature of the foreshore, for he contends that a strip of mud or sand might form a barrier sufficient to prevent *Echinus* from reaching a suitable shore. On examining this statement, however, and in the light of experiment it is found that the fore-shore is of little or no consequence. *Echini* kept by me in aquaria whose bottom was covered with sand had no difficulty in moving about over it. It is not suggested that the specimens made much successful use of their tube-feet, but their spines propelled them adequately. There are several records of specimens dredged from a muddy or sandy bottom. It is possible to believe, on the other hand, that if a foreshore of sand extended a great distance and was very barren of vegetation it might act as a barrier, but in such a case it would be a food barrier, not a locomotion barrier.

This mistaken idea regarding the ability of *Echinus* to cross mud or sand no doubt arises from the impression one gets in holding a living specimen in the hand. It is undoubtedly very heavy, but the weight is largely due to water. The density of the animal relative to sea-water is really very low, as the following measurements show:

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Large specimen: | height 8·9 cm.; | | diam. 10·1 cm.; | | | density = 1·19. |
| Medium specimen: | „ | 7·2 | „ | „ | 8·2 | „ | „ = 1·29. |
| Small specimen: | „ | 4·6 | „ | „ | 6·0 | „ | „ = 1·09. |

The average density of eight specimens was 1·12. The weighings were carried out with a spring balance, so that it was not necessary to remove the specimens from the sea for longer than was needed to weigh them in air.

### (e) *Temperature.*

*Echinus esculentus* is known to live at temperatures ranging from 4·2° C. in the deeper waters (13) to 17–18° C. on the north-east corner of Spain where it is found as a littoral species throughout the year (11). Elmhirst (3) states that

there is a general shoreward migration of *Echinus* in the early part of the year—a spawning migration. Orton (**2**) says that "the need for migration may vary in different localities. It is possible, for instance, that sufficiently high temperatures may occur during a great part of the year below low water in the South of England." This, of course, leaves the Mousehole exception still unexplained, and the more important case of the Bay of Bidassoa and Spain. On Orton's argument *Echinus* ought not to appear near low-water mark at all in the latter places.

Nor can it be maintained that the urchin appears above low-water mark on the British coasts at those places where low water (spring tides) falls during the coolest part of the day. A glance at Table 2 will make this obvious. In fact, from the table it would appear that in the most heavily populated area of Britain (the west coast of Scotland) low water (spring tides) falls at the hottest part of the day. The littoral range of the urchin is so great that it does not seem possible to correlate it with a temperature factor. The average summer temperature of the inshore water of Finmark is 10° C., so that the *Echinus* experiences a range of some 8° C. between its northern and southern horizontal limits and a range of 13·5° C. between its vertical limits.

Table 2.

| Locality | Time of low water (spring tides) hours | Locality | Time of low water (spring tides) hours |
|---|---|---|---|
| Mousehole | 13 | Rispond | 15 |
| Cullercoats | 11 | Tressa Wick | 15 |
| Robin Hood's Bay | 11 | Clyde area generally | 19 |
| St Andrew's | 09 | Loch Sunart | 12 |
| Port Erin | 06 | Kyle Akin | 13 |
| | | Loch Inchard | 16 |

### (*f*) *Currents.*

The course of the Atlantic Drift from Portugal northward is associated in a remarkable way with the littoral distribution of *Echinus esculentus*. This current strikes the European coast near Cape Finisterre (Spain) which divides it into two, one arm going southward along the west Spanish and Portuguese coasts, the other travelling along the north coast of Spain to be deflected northward in the Bay of Bidassoa (Fig. 1). A small offshoot from the latter current enters the mouth of the English Channel but swirls round towards the south Cornish coast in the region of Mousehole and is deflected out of the Channel.

The main northward stream passes up the west coast of Ireland and round the north. I find it very difficult to believe that this urchin is not a littoral species in suitable localities on the West Irish coasts but I have to admit that I can find few definite records. Farran (**16**) in his survey of Blacksod Bay records it from all parts of the bay, which is very shallow, but he does not give a specific instance of its occurrence anywhere.

Nichols (**21**) says: "A large specimen found by shore collecting near harbour of Clare Island, moderate sized specimens at Kinnacorra, etc., and a few small specimens dredged in 5–6 fms. off harbour. A large specimen also on the shore of Annagh Island." While Kemp (**22**) reports the urchin as being "commonly

Fig. 1. Map showing shore distribution of *Echinus esculentus* in relation to the North Atlantic Drift.

found when shore collecting" at Baracladdy, Glassilaum Rocks and Lecknascona, in Co. Galway.

It is perhaps interesting to note that Hartwig (**17**) refers to them as being used for food on "our" coasts. Since, a few lines before, he is writing of Co. Clare, Ireland, the allusion is, at least, suggestive.

The current then passes towards the west coast of Scotland. It is probable that as the current passes the entrance to the Irish sea a small branch may be drawn southward, through the narrow deep channel between Ireland and Scotland, to be lost in the region of the Isle of Man. The main current passes up the Coast of Scotland, along the north and down the east. At about the latitude of Flamborough Head it sweeps east and north towards the most southerly end of Norway where it is deflected up the west coast of Norway by the current from the Baltic. At the northernmost point of Norway the current turns sharply westward again.

Thus the distribution of the current coincides very closely with the littoral distribution of the urchin, while the negative distribution with the absence of the current makes an equally interesting picture. The Atlantic Drift does not touch the south-east, south (with one exception), nor west English coasts, nor the Welsh coast which seems to offer a particularly suitable type of shore for *Echinus*; yet the urchin is completely absent.

Since the presence of *E. esculentus* in the littoral zone is associated with the presence of the North Atlantic Drift, it seems reasonable to try to discover what factor or factors, if any, possessed by the current are the controlling factors. Obviously it cannot be temperature since the current loses heat steadily as it passes northwards, for there is a mean surface difference of 10° C. between the sea at Cape Finisterre and the North Cape (**18**). The high salinity of the drift-water might conceivably be an influencing factor. This would give a perfectly valid reason on the Spanish coast, the southern west coast of France (the dilution due to fresh water from the great rivers, Garonne and Loire, will tend to lower the salinity from the mouth of the former river northwards, and might also account for the low salinity in the English Channel). There is always a small protrusion of water of higher salinity (about 35·3 per mille) almost throughout the year near the south coast of Land's End (**18***a*). North of a line from Land's End to the Irish coast the water is of lower salinity. The west coast of Ireland and Scotland are again subjected to the direct effect of the current and, presumably, to the higher salinity. The Norwegian coast, however, is different. There the salinity close inshore is definitely low (below 34 per mille), so it would seem that higher salinity of the water is not a constant associated factor, for this figure is lower than the English Channel where the urchin does not occur as a littoral form.

### 5. Comparison of forms.

It only remains to make a comparison between the individuals taken on the shore and those taken in deep water. On the north-west coast of Scotland I have always noticed that the intertidal urchins were distinctly larger than those from the bottom. That both sizes are mature I know because I have eaten specimens from both zones. M. Paul Arné (**11**) in writing to me on this subject mentions that this curious gradation of size occurs in south-west

France and north Spain. More recently H. B. Moore (**19**) has remarked this fact amongst the urchins of the Isle of Man. He, however, seems to indicate that, since no really small (young) specimens are found in the higher zones, the vertical migration is a general feature associated with increase in size.

It is an extremely interesting fact that it is always large specimens which range up to the intertidal zone and one might be liable to conclude that the urchins tended to migrate up shore as age increased. In general, however, that cannot be so, for at many places where *Echinus* does not occur as a littoral species large specimens may be found in the off shore waters. I refer, of course to places whose adjoining shore would seem to be a suitable habitat for the urchin. Although it is impossible to equate size-grading with depth-grading in general, nevertheless it is possible to do so in a more particular way: some individuals, as they grow larger, tend to move into the intertidal zone provided the shore type is suitable.

Thus we have a certain group—a variety—which behaves in this characteristic way. This variety is not known to be in any way structurally different from other large specimens of *Echinus esculentus*, but at those places where the Atlantic Drift reaches a coast of suitable type the animals move up to the littoral zone.

## 6. Annual migration.

Elmhirst states that there is a general migration of *Echini* shoreward in the early part of the year. This may be so but, if it is, I suggest that it is only a partial migration at best and probably varies in intensity in different localities, due to small physical changes such as extra cold or extra hot weather, decrease of salinity caused by much rain, etc. Arné (**11**) reports that the urchins of the Laminarian zone in the Bay of Bidassoa are to be found there throughout the year. Also, Moore (**19**) shows by the tables recording the gonad volume that the urchins are found on the Breakwater during every month of the year with the exception of December. However, during that month he does not record their absence but merely a lack of data.

## 7. Summary.

1. The range of *Echinus esculentus* is very extensive.

*Area*: It is known to occur in the North Atlantic generally.

*Littoral*: It extends from Finmark in the north of Norway to the north of Portugal, and is always associated with the presence of the North Atlantic Drift.

*Depth*: It extends from the littoral zone to 1264 m.

*Temperature*: Vertically its temperature (actual) limits are 4·2–18° C. Horizontally its temperature (mean yearly) limits are 5–15° C. (**18**).

*Salinity*: From 36·0 per mille at Finisterre to less than 33·5 per mille on the Norwegian coast.

2. The extent of this range is very great and must be almost unique for several reasons, viz.:

(*a*) Its vertical range would indicate that its food material varied from (on the littoral zone) Algae, etc., to (at 500–1200 m.) such dead matter as fell from the upper layers.

(*b*) Although the temperature range is not in itself very startling it is by no means usual.

(*c*) Despite the fact that large specimens are taken in trawls from many localities it is a peculiar fact that the specimens which are taken from the intertidal zone are larger than those which occur lower down in the same area.

(*d*) Small specimens are seldom, if ever, found in the intertidal zone.

There is thus no obvious simple factor controlling this very varied distribution and one can only conclude that the individuals under examination do not belong to a homogeneous group but that there are in all probability, several forms classed together under the name of *Echinus esculentus*.

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# EPIZOOTICS AMONG FISHES AND REPTILES ON THE AMAZON AND ORINOCO

By J. G. MYERS.

During late December 1930, and early January 1931, the town of San Fernando de Apure, situated on the right bank of the wide Apure River, a primary tributary of the Orinoco, was pervaded by the stench of dead fish, whose odour was carried across the river flats by the prevailing north-east wind. A short journey up river showed the banks for long stretches piled with a continuous wide layer of dead fish, including great circular rays and several giant cat-fish with heads a foot wide, and many alligators (*Caiman niger*). Caracaras and black vultures were busy, vigorously scratching the sand away from the buried fish (which were juicier) with their feet, like barn-door fowls. The turkey buzzards, equally abundant, were not observed to use their feet thus. Both vultures were in countless thousands, but they made little impression on the piles of carrion. A large black *mato* lizard (*Tupinambis* sp.) lay on the bank in a dying condition. Although unwounded, it seemed at its last gasp—merely opening its mouth in a feeble gesture of defiance when a boy approached it, but its efforts to crawl were in vain. My men said it was attacked by the "peste" to which also they ascribed the death of the fishes and caiman.

In San Fernando I was informed that at this season, i.e. about the middle of the dry season, with the level of the river already low, exposing wide sand-banks, many dead fish are usually brought down by the current; but this season the quantities are said to be phenomenal, beyond all past experience.

Páez (trans. 1929, p. 65), writing in the 'sixties, records an epizootic which he considered began among the fishes and reptiles and later spread to the domestic stock. His remarks may be translated as follows:

> The value of these animals [horses] has increased considerably, because of the devastating disease which has diminished their numbers during the last few years. Before this they existed in such growing numbers that the hides were exported in great quantities. At that time a good horse cost five dollars, while at present it is 80 to 100 and even more, according to the fancy of the traders. This plague also decimated the other animals of the country, spreading throughout the land like cholera, and not even the fishes of the rivers managed to escape it. This terrible epidemic, which the llaneros call "peste", is believed to have originated in the great virgin forest of San Camillo, at the head-waters of the Apure, owing to the decomposition of the vegetable detritus accumulated in the course of ages. From there, following the course of the river eastwards, the disease continued its ravages among the inhabitants[1] of the towns and ranches of the right bank, attacking each population in turn, the entire province only barely escaping total destruction. To-day, in spite of a cessation of

[1] It seems evident from the context that Páez does not mean the human population.

the mortality, the country, which possessed a most healthy climate, has not recovered its former salubrity, and more or less dangerous fevers have been prevalent ever since, especially at the end of the rainy season. As a result, the rearing of horses has been totally abandoned. The first symptoms of the epidemic appeared in the caimans, whose repulsive corpses could be seen floating beneath the waters in such prodigious numbers that the air and water alike of that beautiful region were poisoned with the stench. It was observed that they were attacked first by a violent paroxysm of coughing, followed by a black vomit which forced them to leave the waters and find a grave among the bushes on the banks. Soon after, the disease attacked the fishes and other inhabitants of the water, with such violence that it was feared there would be no survivors. The terrible mortality among them can be appreciated from the fact that for more than a month the rippling waters of the Apure River carried down without ceasing enormous putrefying masses which hid the placid surface from view for several weeks. The next victims were the pachyderms [tapirs?] and it was sad to see the lazy chigüres (*Cavia capyrara*) and the wild deer lifting paralysed hind-limbs, from which the disease came to be known as *derrengadera* [crooked disease].

Not even the monkeys escaped contagion, in spite of their aerial life, and their melancholy cries resounded through the woods like the lamentations of the damned.

It is very singular that while the scourge spared none of the countless troops of horses which trod the savannahs of the Apure and the adjacent plains, neither the donkeys nor the horned cattle were attacked, and only this saved the ranch-owners from the total dispersion of their stock.

In an appendix (pp. 460–7) the disease, referred to as *derrengadera* or *deslomadera*, is described in considerable detail by a physician of Calabozo, Dr A. Llamozas, who studied the epizootic in 1856, more especially in its effects on horses. According to this authority the disease was first recorded in 1826, in the province of Apure. It was at first restricted to the banks of the Apure, but in the spring (i.e. beginning of dry season) of 1833 (October) it appeared in the neighbourhood of Calabozo. It still, however, confined its attacks to low-lying pastures, and horses which were restricted to the higher, drier and barer parts of the llanos escaped the disease. Horses in good condition, not working hard, were the most severely affected. Llamozas states definitely that:

the season when the disease develops most is that when the waters retire [from the annually inundated areas], which makes it seem probable that one of the causes lies in the putrid and pestilential miasmata given off by the deposits of stagnant water accompanied by animal and vegetable putrefaction.

The final conclusion of this authority is that the disease is a form of myelitis. The inflammation occurs at the point "where the spinal cord begins to divide to form the tail of the horse". The appearance, red and injected, of that part, the paralysis of the muscles served by it, the paralysis of bladder and rectum, the fever and other symptoms described, are considered sufficient proof of this diagnosis.

It is apparent that the disease attacking equines was *mal de caderas*, a well-known epizootic among horses, caused by a trypanosome.

In another place Páez (p. 86) describes a different type of mortality among fishes, which he seems to believe to be an annual one in the hot season, when the water is deprived of much of the oxygen. "Their carcases may then be seen

floating in the water by thousands, while the beach is strewn with their bones, especially their bristling jaws, which render walking barefoot on the borders of lagoons extremely dangerous." He also describes, on p. 291, the "*miles, millones*" of various fish which perish annually and fill the air with stench when the lagoons and savannah pools dry up. That excessive drought may thus cause mortality even among crocodilians is shown by the report of Gadow (1909, p. 447): "When during a prolonged drought on the island of Marajó, at the mouth of the Amazon, the swamps and lakes were dried up, the alligators migrated towards the nearest rivers, and many perished in the attempt. On one farm were found 8500 dead, and at the end of Lake Arary more than 4000."

Turning now to the Amazon river system, we find similar records of widespread mortality among alligators and fishes. Spruce (vol. 1, pp. 114, 118) twice makes observations on the subject:

> At about the same time (1850) there was a great mortality—a sort of murrain—among the alligators in lakes lying to north of the Amazon, a day's journey from Santarem; but it fell short of what Captain Hislop recounted to me as having occurred many years before, when it was computed that no fewer than a thousand alligators died in the Tapajoz, and floated down to Santarem, where so great was the stench of their decomposing carcasses that the principal merchants had all their boats and men employed for some weeks in towing them down the river to a safe distance below the town. (Vol. 1, p. 114.)

Some further remarks by Spruce may have a bearing on these epidemics:

> As the annual rise of the Amazon is somewhat higher than that of the Tapajoz, and as the latter begins to ebb a little earlier, the waters of the Tapajoz are dammed back by those of the Amazon, and are thus rendered nearly stagnant for several weeks, about the time of highest flood and beginning of ebb. During that period they become unfit for culinary purposes, in consequence of the admixture of yellowish-green slime, called *limo*. I examined the latter with a microscope and found it to consist chiefly of decomposed Confervae, with a very few Diatoms intermixed. It originates in small lakes and sluggish *igarapés*, whose mouths, connecting them with the Tapajoz, become dried up in summer; and, when they are reopened by the swelling rains, the *limo* which had accumulated in them whilst stagnant is discharged into the river....No doubt this slimy water is very unwholesome....I have seen a similar effect from a similar cause in the river Atabapo, a tributary of the Orinoco. (Vol. 1, pp. 118.)

An earlier record is that of von Martius (vol. 3, p. 1020), who mentions it among the results of an abnormally high flooding by the river:

> Especially remarkable besides was the great mortality which these extraordinary inundations produced among the snakes, caimans, and fish, which inhabited the lakes and standing waters along the River. This was partly caused by the putridity of other dying animals [cattle], but also by the contamination of these standing waters with the Amazon floods. The settlers along this River are unanimously of the opinion that the water itself, because it is well mixed and in motion (*por ser bem battida*) is preferable to most other drinking water, as soon as the earthy matter which is contained in it is allowed to settle....[The author proceeds to show that the water of the lagoons and canals ought to be less salubrious than that of the main stream]....At the same time I should like to deduce the increased mortality of the [animal] inhabitants during the long-continued high water in the River from the mixture

with its waters. Although caimans and large snakes occur also in the River itself, the greater number live in the collections of water by the sides, and come only in the running water when they go hunting, or are attracted by the smell of animal remains which have floated from the neighbourhood of the settlements and in particular of the fisheries. (Transl. from the German.)

Bates (p. 289) observed a similar mortality among fishes on the Upper Amazon (Solimões) and ascribed it to the low temperature of the periodic "friagens" or cold spells caused by southerly (or as other observers state, south-west, and south-south-west) winds, which cause a very sudden and quite considerable drop in the temperature. "The temperature is so much lowered that fishes die in the river Teffé, and are cast in considerable quantities on its shores. One year I saw and examined numbers of these benumbed and dead fishes. They were all small fry of different species of Characini." This is evidently a much more local effect than the widespread Venezuelan epizootics described above; but it is also noted by Spruce (1908, vol. 1, p. 188) who saw this happen at a place where the cooler waters of the Amazon met the heated waters of the Ramos. He remarks that:

This phenomenon takes place every year, not only in the Ramos, but in many other periodically-closed channels of the Amazon.

On the Rio Negro, in 1839, Robert Schomburgk (trans. pp. 181–2), after describing forest fires due to the great drought, says:

The heat and drought had become just as prejudicial to the fish as to the vegetation: they lay in immense quantities on the dry sandbanks and polluted the surrounding atmosphere.

Although I saw no birds affected on the Apure River—in spite of the fact that various herons and cormorants were especially abundant—yet I have been struck by the great similarity to duck-sickness, as reported in the United States. Thus Lincoln (1929, p. 103) describes the drying shores of a lake "strewn with dead and sick ducks and shore birds.... I estimated at that time that there were about 1000 dead or dying birds to each mile of shore line, and I was told that the shore line was about 20 miles in extant." This observer believed that the birds were suffering from alkali-poisoning, but later found another drying lake with its shore "literally incrusted with alkali" but no sick ducks. Kalmbach (1932) investigated the disease and was able to prove that it was botulism, the organism of which, *Clostridium botulinum*, was incubated in the decaying organic matter of the drying lake shores. Finally, it may be worth noting that similar large-scale epidemics have been noted among hippopotami in the Kasai River (for records see Elton, 1931).

## Summary.

The little that is definite may be summed up as follows:

(1) Widespread epizootics affecting fishes and aquatic or riparian reptiles occur in the main streams of the Orinoco and Amazon water systems.

(2) These epizootics are periodic, associated with the retirement of the waters but distinct from the mortality necessarily caused by the complete drying up of ponds, in that they occur in the main river, in the presence of abundant, freely-flowing water.

(3) There is some evidence that the epizootics are associated with drought conditions, which are themselves periodic in northern South America, though their periodicity has not yet been worked out.[1]

(4) In the absence of any bacteriological or pathological studies, it may be tentatively suggested that certain features of the epizootic are reminiscent of botulism.

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[1] The observations of Koch-Grünberg (1917, vol. 1, p. 6) and of Bates (1892, p. 148) definitely favour a ten-year cycle.

# POPULATIONS, TERRITORY AND INTERRELATIONS OF THE ANTS *FORMICA FUSCA, ACANTHOMYOPS NIGER AND MYRMICA SCABRINODIS* AT GARFORTH (YORKSHIRE)

By WALTER PICKLES.

(*With Plate 2 and 2 Figures in the Text.*)

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## 1. Introduction.

The study of territory relations and population density among ants has received little attention in this country, but the observations of Elton (1932) showed that territory is very well marked in one species of ant (*Formica rufa*). In the present survey, observations were made on three other species, in order to find out whether territory behaviour was of importance between different species, and actual counts of nest populations in different territories were made. The work has been going on since 1932 and is still in progress.

## 2. The area under observation.

The area under observation is situated at Garforth in Yorkshire. The ground is somewhat rough, though level, and composed of clay mixed with the refuse from a now dismantled colliery nearby. The vegetation is chiefly young birch (*Betula alba*) and elder (*Sambucus niger*). Amongst the common ground plants, the most abundant are wild strawberry (*Fragaria vesca*), and *Veronica officinalis*, with a great preponderance of rosebay (*Epilobium angustifolium*), lichen (*Cladonia*) and various mosses. The species of ants studied were *Formica fusca* L., *Myrmica scabrinodis* Nyl., and *Acanthomyops* (*Donisthorpea*) *niger* L. These were kindly verified by Mr H. J. St K. Donisthorpe. The area of the ground is about $56 \times 48$ yds., giving an area of roughly 2688 sq. yds.

### 3. TERRITORY.

#### (*a*) *Formica fusca.*

In this area twenty-two nests were located and marked; two of *Formica fusca*, ten of *Myrmica scabrinodis* and ten of *Acanthomyops niger*, as shown on the accompanying map (Fig. 1). By observing the various distances travelled by ants from their nests, the *Formica fusca* were found able to travel farther than the other two species. From nest 13 (*F. fusca*), I observed an ant to travel to a maximum distance of 26 ft. Within a circle of this radius, these ants are very active; but on no occasion have they been observed to travel farther than this. The points on the map show that two nests of the other two species are within the foraging area of nest 13.

Within this area, the ants from nest 13 had a definite preference for travelling north-east to a clump of rosebay plants on which were large numbers of aphids. Throughout the year this "path" is free from vegetation, and runs to the limit of the foraging area, i.e. 26 ft. from nest 13.

One or two observations at nest 22 (*F. fusca*) in no case yielded a greater area covered than mentioned above.

#### (*b*) *Myrmica scabrinodis.*

In the case of *M. scabrinodis* several nests were observed and recorded. In nest 5 the ants had a definite preference for travelling south-east; but in this case the ground slopes with a north and north-east direction, and is nearly devoid of vegetation (in this direction). The greatest distance noted was 20 ft.

Text-fig. 1. Positions of the nests, and the maximum distances travelled by ants at different times. *Myrmica scabrinodis*: nests ×, max. distances ●; *Acanthomyops niger*: nests ⊗, max. distances ⊙; *Formica fusca*: nests ⊠, max. distances ⊡.

in a south-westerly direction. At nests 2 and 12, the other two nests used for territory determinations, this distance (20 ft.) has not been exceeded, the greatest distances in these cases being: nest 2, 16 ft. and nest 12, 13 ft. The actual area used for foraging is greater in these latter cases, because it is carried on about equally in all directions from the nest. In the case of nest 5, as mentioned above, a preference is shown for an area south-east of the nest.

Nests 1, 2, 12 and 18 were used purely for population determinations, and nests 14, 19, 15 and 16 were temporary nests, the latter two only existing for a few days; whilst nest 19 existed for several months during the summer of 1933 (see more detailed account later). Nest 15 was located and marked on October 31st, 1932; but by November 20th not an ant could be found, although no external disturbance of the soil was to be seen.

### (*c*) *Acanthomyops niger*.

With regard to *A. niger*, three nests (4, 9 and 20) were used for territory determinations, four being used for population determinations. Nest 11, although large and flourishing on August 8th, 1932, had disappeared by October 30th, 1932. As in the case mentioned above, no external disturbance, such as scratching up, appeared to have taken place. Nests 3 and 21 were only very small temporary nests, the former being in existence only one day during August 1932 and the latter for a few days only during the summer of 1933 (June 25th to July 9th).

*A. niger* in this area appears to occupy less territory than either of the other species. Nest 4 had a greater area than the other nest (No. 9), the greatest distance travelled by ants from nest 4 being 10 ft., whilst the maximum distance at nest 9 was 5 ft., with a preference for a north north-easterly direction. This nest (no. 9) is situated in the feeding (foraging) area of nest 2 (*Myrmica scabrinodis*), the latter ants have been observed on many occasions crawling on the nest mound of no. 9. This phenomenon has occurred both with and without the presence of the home ants (*Acanthomyops niger* from nest 9).

The distances travelled by *A. niger* appear small, and the ants themselves are not so active as the other two species. As a comparison to these distances may be quoted a distance travelled by the same species of ant on Wandsworth Common, near London, where on June 10th, 1934, at 10 a.m. I noticed a stream of these ants to travel from the railway embankment through the railings, across an asphalt path approximately 5 ft. wide and up a sycamore tree. The ants were "swarming" on the branches 18 ft. or so in length. The total distance travelled by these ants away from the nest must have been in the region of 40 ft. or more.

Evidently the northern climate and possibly the proximity of a manufacturing district may have some negative action on the activities of this species of ant. The maximum distance travelled by this ant is taken as 10 ft.

*Photo. W. Pickles*

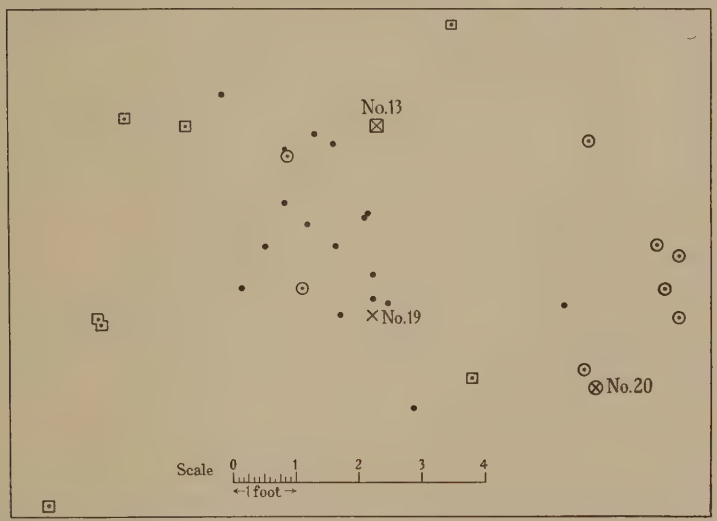
Phot. 1. General view of area under observation, showing in the foreground nests 9 (left) and 2 (right). The Rosebay (*Epilobium angustifolium*) is in full flower.

*Photo. W. Pickles*

Phot. 2. Nest no. 1 (*M. scabrinodis*) showing the prevalence of wild strawberry (*Fragaria vesca*); mound and entrance to the burrow of the bee *Halictus rubicundus*, in the foreground. (June 1st, 1933.)

### 4. Relationships of the three species.

The three species, *Acanthomyops niger*, *Formica fusca* and *Myrmica scabrinodis* seem to live closely together, and friendly relations exist between them. The nests in the area have been constant (the parent nests at least). and this seems to show that the three species have little or no effect on each other. Evidence to support the view that they live "on friendly terms" may be given as follows. During March 26th, 1933, in the neighbourhood of nest 13 (*Formica fusca*), I noticed several specimens of *Myrmica scabrinodis*. One of these went down a hole; there I found a small nest (about fifty individuals). This was situated 3 ft. 0 in. from nest 13. A few days later, I similarly dis-




Text-fig. 2. The common territory of the three species of nests 13, 19 and 20. The points show the maximum distances within the small area travelled by the ants at different times. *Myrmica scabrinodis*: nests ×, max. distances ●; *Acanthomyops niger*: nests ⊗, max. distances ⊙; *Formica fusca*: nests ⊠, max. distances ⊡.

covered a nest of *Acanthomyops niger* 5 ft. 5 in. from nest 13 and 3 ft. 9 in. from the above-mentioned nest of *Myrmica scabrinodis*.

From this date until the end of July 1933, these three nests were co-existent. Specimens from each nest would, during their foraging excursions, crawl over the nest or nests of the other species (see accompanying diagram). As a matter of fact, I have seen specimens of *M. scabrinodis* and *Acanthomyops niger* meet, tap antennae, and then pass on. Only on one occasion have I seen anything which resembled hostility. That was on April 14th, 1933, when a *Formica fusca* was found carrying a specimen of *Acanthomyops niger* about 4 ft. 3 in. from nest 13. The former dropped the latter and returned to nest 13 "empty-handed" and the latter ran away to its own nest (No. 20).

From this evidence it seems very probable that the three species live peacefully together, even though the territory of one nest overlaps that of another. Each nest seems to exist independently and indifferently to the other nests in the area.

### 5. Responses to temperature and weather conditions.

The activity of all the species of ants studied depends directly on the temperature and weather conditions. Hot, somewhat sultry, weather favouring activity, and cold weather suspending it totally. The warmth of the ground determines activity, not merely the warmth of the air; for instance, days when the air is warm and the sun is warm will produce no activity if the ground is cold or very wet. During the autumn of 1932 I observed that the activities of the ants were finally suspended for the winter by October 23rd. On this date I noticed only one solitary *Myrmica scabrinodis* ♀ from nest 5. This species was the last to retire for winter—the first being *Formica fusca*. In the following year (1933) I first found signs of activity on March 12th. On this date specimens of *Acanthomyops niger* were very active, foraging from nest 9. By March 26th specimens of *Myrmica scabrinodis* were to be observed foraging near nest 13 (*Formica fusca*). No evidence of activity from *F. fusca* was found until April 5th when the soil temperature was 10° C. (50° F.).

On the whole, the ants seem to live nearer the surface of the nest in summer than in winter. If one opens a nest in summer the "nurseries" are found to be only covered by a thin layer of soil (these statements refer to *Acanthomyops niger*) and the deep chambers are met with at depths of 3–4 in. down. In winter I never found chambers nearer to the surface than $3\frac{1}{2}$ in., and the deep chambers were at least 8–9 in. deep.

Wind appears to play a great part in determining the activity of ants, both through its direction and velocity. During a strong west wind of gale force very little or no activity will be found—this I have noted time after time. Often on visiting the ants on a brilliantly sunny, boisterous day, I have been disappointed in not finding a single ant of any species walking about. As previously mentioned, the greatest activity occurs on hot sultry days, with a minimum of wind.

Besides being affected by weather conditions, the presence of ants' nests modifies the soil temperature of the area where they are situated. On February 19th, 1933, on visiting the area under observation, after a downfall of snow, I found that the snow had melted on the southern slopes of all the nests by 3 p.m. on that date. This phenomenon may possibly have some slight effect on the vegetation on the nest mounds. Another possible effect of the presence of nest mounds was observed on May 22nd, 1933, when it was quite easy to pick them out, each being nearly covered with wild strawberry plants (*Fragaria vesca*) which were in full bloom. The intermediate spaces were very sparsely covered with strawberry plants. The heat generated by the ants may have some effect on the growth of this plant. This bloom lasted until early June.

Although 1933 was a remarkably hot year, and during the early summer the ants were very active, towards the middle of August they were less active than at the same period the previous year. This was probably due to the drought, as most of the plants on the area, especially rosebay (*Epilobium angustifolium*) were withered and dried up. On the rosebay particularly, large numbers of aphids are usually reared, but during the period just mentioned very few aphids could be found owing to the condition of the plants.

## 6. POPULATIONS OF THE NESTS.

The population of an ants' nest does not appear to be determined by the size of the nest mound. In a nest, which at first sight seemed large, a relatively small population has been found, and *vice versa*. The populations, given below, were obtained by counting the living inhabitants. An error has crept in through the number of ants which escaped whilst the nests were being dug up, packed and carried home. In the following table a column has been provided to give an estimate of the approximate number thus lost.

### (*a*) *Formica fusca*.

| No. of nest | No. of ants actually counted | No. of ants estimated as lost (approx.) | Total no. of ants | Superficial area of nest mound | Date |
|---|---|---|---|---|---|
| 13 | 2746 | 100 | 2846 | 3·1 sq. ft. | 17. vi. 33 |
| 22 | 2189 | 100 | 2289 | 7·1 sq. ft. | 3. xii. 33 |

### (*b*) *Myrmica scabrinodis*.

| No. of nest | No. of ants actually counted | No. of ants estimated as lost (approx.) | Total no. of ants | Superficial area of nest mound | Date |
|---|---|---|---|---|---|
| 18 | 156 | 30 | 186 | 9·6 sq. ft. | 26. xi. 32 |
| 12 | 1253 | 50 | 1303 | 9·6 sq. ft. | 14. ix. 34 |
| 1 | 547 | 50 | 597 | 7·1 sq. ft. | 21. ix. 34 |
| 2 | 2292☿ 11♀ | 50 | 2353 | 4·9 sq. ft. | 25. ix. 34 |

### (*c*) *Acanthomyops niger*.

| No. of nest | No. of ants actually counted | No. of ants estimated as lost (approx.) | Total no. of ants | Superficial area of nest mound | Date |
|---|---|---|---|---|---|
| 7 | 258 | 50 | 308 | 4·9 sq. ft. | 20. xii. 32 |
| 4 | 6570 | 100 | 6670 | 4·3 sq. ft. | 15. i. 33 |
| 8 | 2061☿ 90♀ | 50 | 2201 | 4·9 sq. ft. | 4. ix. 34 |
| 9 | 3236 | 50 | 3286 | 7·1 sq. ft. | 4. viii. 32 |

The error (third column) of the estimated populations was reckoned on the spot, taking notice of the activity of the particular nest at the time. For the size of the nest more *Formica fusca* were lost due to their greater activity.

The populations represent the more or less stationary numbers except nest 8 which contained ninety virgin queens; the "swarming" times not being included.

Of the three species of ants, the *Acanthomyops niger* nests seem to be the most populous, being followed by the *Formica fusca* nests. As there were only two nests of the latter species present, fewer determinations had to be made. The smallest populations belong to the *Myrmica scabrinodis* nests. They seem very small in comparison with the others—yet they are the most conspicuous ant in the area, and would, therefore, lead to a wrong deduction that they were the commonest ant. As the counting has been done outside the "swarming" period, worker ants alone have been found, except in the case of nests 2 and 8 mentioned above.

Concerning the distribution of the ants in the nests, this has varied with the years, and may possibly be due to the two drought years 1933 and 1934. The nests dug up in 1932 and the early part of 1933 (e.g. nest 4) consisted of chambers connected by galleries—the mass of the population being in the chambers. The nests dug up in the two latter years (1933–4) displayed rather a different state of things. Many of the chambers were deserted, and the ants found more or less at random in the nest—except near the boundary, where the original clayey layers of the ground had not been disturbed, and had retained a little moisture. The ants had in several cases excavated new chambers here. In the case of *Myrmica scabrinodis*, most of the ants in nests 1 and 12 were found amongst the rootlets of the grass covering the mound, and round the edges of the nest mound as mentioned above. In all the three species, the ants have a definite preference for excavating their chambers in the clayey layers of the ground, rather than in the earthy layers, possibly due to the extra retentivity of moisture and firmer structure of the clay.

### 7. Density of population.

The following tables give the total ant population of each of the three species, the territory covered by each of them, estimated by taking the maximum distance travelled, to be the radius of a circle of foraging ground of which the nest is the centre. From this the *lowest density* of population (population divided by area under census) and the *economic density* (population divided by territory) are given in the other columns, each of the species being tabulated separately (see Elton, 1932). *Formica fusca*: Only two nests discovered and therefore both used for determinations. *Acanthomyops niger*: Four nests used for determinations, and, since seven permanent nests existed, an average population, based on these four determinations, is used for the density calculations. *Myrmica scabrinodis*: Four nests were used for population determinations, whilst seven permanent nests existed. The density calculations again were based on an average population per nest as with *Acanthomyops niger*.

*Formica fusca.*

| 1 Total population | 2 Territory per nest: given by $\pi r^2$ { $r$ = maximum distance travelled by ant | 3 Economic density = Total population / Total territory | 4 Lowest density = Total population / Area of census* |
|---|---|---|---|
| 4935 | 236 sq. yd. | 10·45 per sq. yd. | 1·835 per sq. yd. |

*Myrmica scabrinodis.*

| 1 Total population of four nests | 2 Average no. per nest | 3 Total population est. for seven nests | 4 Territory per nest: given by $\pi r^2$ { $r$ = maximum distance travelled by ant | 5 Economic density = Total population / Total territory | 6 Lowest density = Total population / Area of census* |
|---|---|---|---|---|---|
| 4439 | 1109 | 7763 | 140 sq. yd. | 7·921 per sq. yd. | 2·888 per sq. yd. |

*Acanthomyops niger.*

| 1 Total population of four nests | 2 Average no. per nest | 3 Total population est. for seven nests | 4 Territory per nest: given by $\pi r^2$ { $r$ = maximum distance travelled by ant | 5 Economic density = Total population / Total territory | 6 Lowest density = Total population / Area of census* |
|---|---|---|---|---|---|
| 12,465 | 3116 | 21,812 | 35 sq. yd. | 89·028 per sq. yd. | 8·118 per sq. yd. |

* Area of census in all the three species is the same and is as follows: 2688 sq. yd.

The figures which are given under the populations of the nest mounds can be taken as representing the *greatest density* of population: as the nests were all dug up in the evenings, the population would be practically at a maximum.

From the tables it will be seen that the commonest ant is *Acanthomyops niger*, followed by *Myrmica scabrinodis*, and the least common is *Formica fusca*.

### 8. Food and foraging.

All three species of ant seem to live chiefly on the excreta of aphids, which are exceedingly numerous on the rosebay plants in the region round the nests. The ants travel from the nest, climb the rosebay plant, and proceed to tap the aphids or search the surface of the leaf for spilt "honey-dew". On August 23rd. 1934, I observed some specimens of *Acanthomyops niger* on a rosebay leaf, licking honeydew. They were followed on the same leaf by specimens of *Formica fusca* and *Myrmica scabrinodis*, and later a wasp (*Vespa vulgaris*) alighted on the same leaf and began licking where the ants had been.

Specimens of aphids from *Epilobium angustifolium* were submitted to Mr Frederick Laing at the British Museum of Natural History. They were difficult to identify owing to being all young ones. He states, however, that they are a species of *Aphis*, rather similar to but possibly not the same as *A. epilobiina* Walker, known from the rosebay.

Besides gaining nourishment in this way, the three species are also partly carnivorous, as on many occasions I have found them carrying the remains of insects—elytra, etc. The following actual records of prey were made:

| *Acanthomyops niger* | *Myrmica scabrinodis* | *Formica fusca* |
|---|---|---|
| Aphids | *Abax ater* | *Pterostichus madidus* |
| *Agriotes pollidulus* (elytra) | *Olisthopus rotundatus* (elytra) | *Odynerus parietimus* |
| Wasp (*Vespa vulgaris*: abdominal segments 1 and 2) | **Pterostichus madidus* (elytra) | |

The elytra marked (*) were found amongst a mass of dismembered remains of *Myrmica* and *Formica fusca* some 3 ft. from nest 5 (*Myrmica scabrinodis*). At first I thought this mass was a kind of cemetery for dead ants of this nest. On finding the elytra of *Pterostichus* present I presumed that it might be a refuse dump of indigestible parts of insects used as food. On submitting these elytra, etc. for confirmation of species to Dr Blair of the Natural History Museum, he suggested that possibly they were originally in the pellets of an owl, and that one of these pellets has possibly been broken up by the ants. So far as I have investigated, I have never seen any of the ants carrying pieces of flesh other than pieces of insects.

On July 9th, 1933, I decided to test the ants with fruit, so on visiting the area I took with me several cherry stones, with adhering pieces of fruit. I placed one of these stones near a specimen of *Formica fusca*: eventually it touched the stone with its antennae, and immediately it began biting off pieces of the fruit. Later several specimens of *Acanthomyops niger* and *Myrmica scabrinodis* came to the stone; but none took any of the fruit. These were

followed by another specimen of *Formica fusca* which also ate the fruit off the stone. Evidently, then, the latter species have a "taste" for fruits, which may augment the insect and aphid diet above mentioned. Possibly (this is entirely a suggestion) *Formica fusca* may eat the wild strawberries growing on the area in their season.

The aphid, mentioned under *Acanthomyops niger*, was not used for obtaining honeydew, but was a dead one which was being carried to the nest—not from it—therefore it seems as though it was being used as food.

In experimenting with an artificial nest of *Acanthomyops niger* I found that the ants readily licked up honey, but that pieces of flesh were hardly touched. Flesh used included small pieces of beef, mutton, pork, mouse, and thrush. This species evidently prefers the remains of flesh on the parts of insects found in its foraging area.

## 9. Acknowledgments.

I wish to thank experts at the British Museum of Natural History who have kindly identified various insects and plants: *Ants*, Mr H. St J. K. Donisthorpe; *Aphids*, Mr Frederick Laing; *Beetles*, Dr K. G. Blair; *Plants*, Mr A. J. Wilmott.

## 10. Summary.

1. Territory. Of the three species studied, *Formica fusca* has the largest feeding territory (236 sq. yd.), with *Myrmica scabrinodis* next (140 sq. yd.) and *Acanthomyops niger* the least with 35 sq. yd.

2. Relationships of the three species. The three species apparently live on good terms with each other and have common foraging territory, e.g. nests 13, 19 and 21.

3. Populations. The most populous nests are those of *Acanthomyops niger* and the least populous *Myrmica scabrinodis*; in the case of the densities of population, whilst *Acanthomyops niger* again heads the list, *Formica fusca* has the second largest economic density, and *Myrmica scabrinodis* the second lowest density.

4. Food. All the species appeared to live on the excreta of aphids cultivated on the rosebay (*Epilobium angustifolium*), together with adhering flesh of dismembered insects. *Formica fusca* was the only species found experimentally to take fruit, and this species may obtain part of its food from the wild strawberry so common on the area.

## REFERENCE.

**Elton, C. (1932).** "Territory among wood ants (*Formica rufa* L.) at Picket Hill." J. Anim. Ecol. 1, 69.

# A POPULATION OF WOOD ANTS (*FORMICA* SP.) AT ABERNETHY

By CYRIL DIVER.

(*With* 1 *Figure in the Text.*)

When staying at Abernethy (near Nethy Bridge, Inverness) during August 1909 I had the opportunity of examining a pinewood which was occupied by a large population of wood ants. As the nests were thickly distributed and the paths made by the ants were easy to trace, I amused myself by making a sketch-map (Fig. 1) of the areas occupied by each of several contiguous nests. This map was made on August 29th, 1909. Unfortunately no details now remain except the original map on which no scale is shown. The relative positions of the nests and the trees were determined by pacing. The record is thus tiresomely incomplete; but in view of Elton's note (1932) it seemed worth while to publish the map with such information as can still be drawn from my memory. No specimens were taken, and, since I was then ignorant of the taxonomic characters of this genus, the exact species cannot be stated. The mounds were large, made of pine-needles and appeared the same as those usually built by *Formica rufa* L.

The area examined was a flat pinewood, on the floor of which, as far as I can remember, there was very little vegetation. Towards the south-east corner of the ground mapped there was a small marshy patch, to the east of which the general level rose some 3 ft. above the rest of the area. Most, if not all, of the trees within the area mapped are shown, whether they were visited by ants or not. The relative sizes of the mounds are roughly indicated on the map. Nest 3*a* (presumably a branch nest from 3) being considerably smaller than the others.

The observation was confined to the mapping of the ant-roads, which were carefully traced for each nest. It will be seen from the figure that in two cases (nests 2 and 4) these roads follow the line of the human paths; in the case of nests 2, 3 and 4 they cross the human paths. From memory it seems highly probable that the human traffic along these paths was very light. At the time the map was made the ant-roads were divided by eye judgment (based on the amount of traffic that appeared to be passing over them) into main roads and smaller roads. In the population examined by Elton, only one of the seven nests mapped showed a regular forking of the roads. In this case all the four main nests have forked roads and it will be seen that the main roads are mostly those which lead to a fork or to more than one tree; but in one case, at least, the main road is marked as continuing after a fork.

In the case of nests 3 and 3*a* there appears to have been a path leading directly between them, and both nests seem to have used the same tree. Whether they shared the same path up this tree or approached it from different sides is not clear. No similar intercommunication between nests appears on Elton's map.

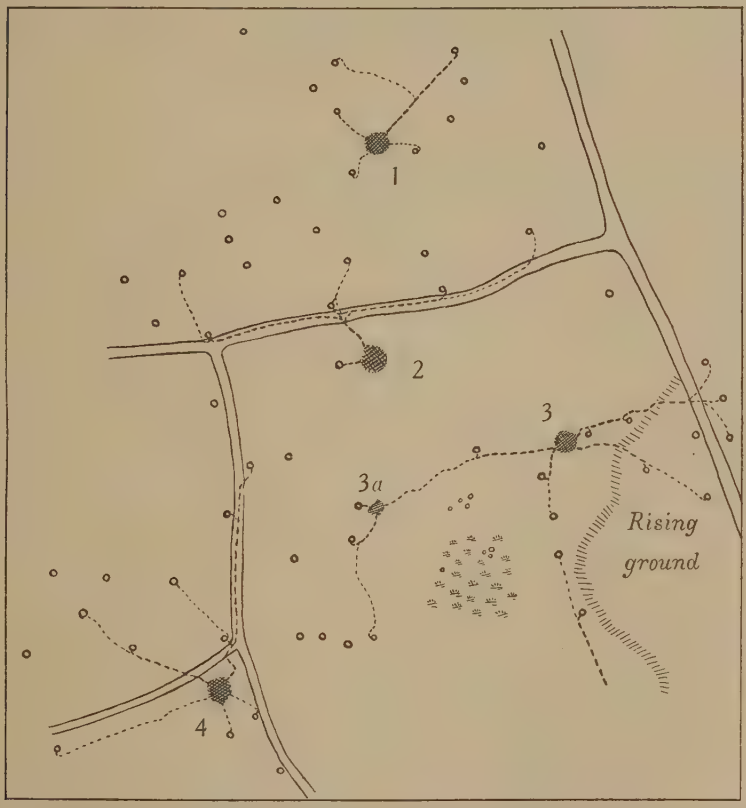



Fig. 1. Sketch-map of part of a pinewood near Abernethy, Inverness (August 1909), showing the distribution of five wood ants' nests and the system of ant-roads leading from each nest. These roads are indicated by the broken lines, the main roads being more heavily drawn than the smaller roads. The human paths are drawn with a continuous line, and the trees are indicated by circles.

The number of trees used by the foraging parties from each nest ranges from four in the case of the small nest 3*a* to ten in the case of nest 3. Although there were three other trees in close proximity to nest 1, the activities of this colony were apparently sufficiently met by the use of five trees. Nest 2 used seven trees, not necessarily those which were actually closest to the nest.

Nest 3 occupied ten trees, or all except one within its territory. Another nest not shown in the chart occupied two trees not far from nest 3. The needs of nest 3*a* were apparently met by four trees, while nest 4 occupied 9. It seems probable from the number of unoccupied trees that the population living in this area was not at a maximum density.

It may be noted that the roads made by the ants are by no means necessarily straight, and that the trees are frequently not climbed on the side directly facing the line of approach. This is well shown in the case of three trees used by nest 1 and two used by nest 4.

REFERENCE.

**Elton, C. (1932).** "Territory among wood ants (*Formica rufa* L.) at Picket Hill." J. Anim. Ecol. 1, 69.

# THE LOW TEMPERATURE LIMIT OF ACTIVITY OF ARCTIC INSECTS

By G. C. L. BERTRAM.

(*With* 1 *Figure in the Text.*)

## 1. Introduction.

The work described in this paper was carried out during August 1933 at the base, in Hurry Inlet, of the Cambridge Zoological Expedition to Scoresby Sound, East Greenland (**8**). I have much pleasure in thanking my companions, the two other members of the Cambridge party, David Lack and Brian Roberts, for their continual help and for catching most of the insects; also Dr J. B. Charcot, without whose kindness the Cambridge party would never have reached Greenland. To Mr J. T. Saunders and Mr Kenneth Mellanby many thanks are due for their advice as to the form and scope of the apparatus used; and to Prof. J. Stanley Gardiner for the loan of materials. I should also like to thank the following specialists who were kind enough to assist by the identification of the insects and spiders: Miss Aubertin (Diptera), Dr F. W. Edwards (Diptera), Dr A. Roman (Ichneumonidae), Messrs W. H. Tams and N. D. Riley (Lepidoptera), Dr O. W. Richards (Apidae), Messrs W. E. China (Hemiptera), G. J. Arrow (Coleoptera), M. Mosely (Trichoptera), and Dr A. R. Jackson (spiders).

## 2. Discussion.

A species of animal is absent from a given area for reasons that may be summarised under two headings, (1) that the animal has never reached the area, and (2) that the animal in question fails to survive in that area. Perhaps some animals, notably birds, do not inhabit certain places owing to their fixity of behaviour, quite apart from the otherwise suitable nature of the habitat. The causes of the animal's failure to survive may be classed as lack of food, natural enemies, or adverse physical conditions. The last may be further subdivided into adverse local conditions (plant association, lack of vegetation, etc.), and an unsuitable climatic environment. In the present paper the relation to geographical distribution of low temperature alone is discussed, and this only so far as it directly affects the activity of adult land arthropods.

It has been shown in certain instances that an insect must get more than a fixed minimal amount of heat in order to complete each stage in its life history. This heat is measured as the sum of the products of the temperatures and the hours for which those temperatures have been in action (**5**, **7**). This pheno-

menon is no doubt an extremely important factor in considering the geographical distribution of arctic forms, but Merriam's (**6**) statement cannot be wholly accepted that "animals are restricted in their northern distribution by the total quantity of heat during the season of their growth and reproduction". Sanderson (**9**) has demonstrated that the direct lethal effect of low temperatures (the average annual minimum probably being the best index of the winter temperature) is the limiting factor in the northward distribution of certain insects at any rate. In some instances this may be true, but on the other hand it should by no means be taken to apply in all cases. However, a detailed summary of the relationship between temperature and geographical distribution is provided by Chapman (**1**).

Insects in the Arctic are not exposed to such very low temperatures as is usually supposed. During the summer months the vegetated areas where they live are rarely subject to temperatures below freezing-point, and commonly the insects are living under stones or vegetation where the temperatures are often several degrees higher than that of the air above. During the winter when the supposedly lethal temperatures are reached (as measured by the thermometers placed well above the ground) the insects, at various stages of their life history, are buried below a thick blanket of snow whose effect is to prevent the ground beneath sinking to a temperature anywhere approaching that to which the outside air may fall.

To quote from Hansen (**2**): "According to Wild (**10**) a snow covering of 30–45 cm. depth will cause a temperature difference of 8-9° C. between the surface of the soil and that of the snow. Thus a sandy surface has a January–February temperature of *c.* −10° C. while the surface below a snow covering of 30–40 cm. has only a January–February temperature of −2° C.; at a depth of 40 cm. the values are −6 and +1° C. respectively. . . .Very convincing and thorough investigations on temperature conditions in snow have been made by J. Keränen (**3**). . . .The snow covering during the months November–April has an average depth of 47·8 cm. and due to this an average surface temperature of −14·2° C. can only cause the temperature at the bottom, i.e. at the surface of the soil to drop to −2·7° C." The extent of this insulation by snow is also well seen in the table below, derived from Keränen (**3**).

The muscular activity of poikilothermic animals is dependent directly on the temperature of their surroundings, especially among the land Arthropoda. In the present paper it is pointed out that the direct effect of low temperatures upon the activity of the adult insect may in itself be a method in which the temperature may exert a limiting action in their distribution.

It is obviously necessary that the lower temperature limit of activity of the adult insects must be surpassed in the environment during the course of the year if the species is to survive in the area at all. For how long a period the adults must be active to complete their mating and egg-laying is not known and is probably very variable, but in many forms the number of eggs deposited

is perhaps dependent directly on the length of the period of activity. An example of this was noted on Bear Island in the summer of 1932 by David Lack and myself when the temperature on only six occasions was apparently sufficient for the ichneumon *Stenomacrus pedestris* Holmg. to be fully active.[1] The temperature that must be reached for emergence to take place may again be different from the lower limit of adult activity and may be perhaps higher. In such a case this temperature might not be reached for some days after the temperature is sufficient for the adults had they already emerged, and so the period of adult activity might be still further curtailed.

*The daily variation in temperature in air and snow at Sodankylä, Finland, on March 19th–20th, 1917.*

(From Hansen, p. 166, after Keränen (**3**, p. 92).)

| Time of day ... ... | 0 | 2 | 4 | 6 | 8 | 10 | 12 | 14 |
|---|---|---|---|---|---|---|---|---|
| Air ° C. ... ... | −35·7 | −37·9 | −39·4 | −40·4 | −34·5 | −20·4 | −15·3 | −12·7 |
| Snow in ° C. 0 cm. | −37·7 | −38·9 | −40·0 | −40·1 | −36·5 | −24·0 | −15·9 | −14·4 |
| −4 cm. | −30·0 | −31·7 | −33·0 | −33·9 | −32·9 | −25·7 | −14·7 | −12·0 |
| −14 cm. | −19·0 | −20·1 | −21·0 | −22·0 | −22·5 | −22·1 | −20·1 | −17·8 |
| −24 cm. | −13·7 | −13·9 | −14·2 | −14·7 | −14·9 | −15·1 | −15·1 | −14·9 |
| −44 cm. | − 7·3 | − 7·4 | − 7·3 | − 7·5 | − 7·5 | − 7·6 | − 7·5 | − 7·7 |

| Time of day ... ... | 16 | 18 | 20 | 22 | 24 | Mean | Range |
|---|---|---|---|---|---|---|---|
| Air ° C. ... ... | −13·4 | −16·9 | −26·3 | −31·9 | −34·4 | −27·6 | 27·7 |
| Snow in ° C. 0 cm. | −20·8 | −28·1 | −32·9 | −34·7 | −36·8 | −30·2 | 25·7 |
| − 4 cm. | −15·9 | −21·0 | −25·1 | −27·6 | −29·6 | −25·1 | 21·9 |
| −14 cm. | −16·6 | −16·6 | −17·5 | −18·1 | −19·0 | −19·4 | 5·9 |
| −24 cm. | −14·7 | −14·5 | −14·2 | −14·0 | −14·0 | −14·5 | 1·4 |
| −44 cm. | − 7·7 | − 7·7 | − 7·7 | − 7·7 | − 7·7 | − 7·6 | 0·4 |

## 3. Experimental work.

In an attempt to investigate these possibilities, and further the possible presence of peculiar powers of retaining adult activity at low temperatures, experiments were carried out in East Greenland during the summer of 1933. A simple form of apparatus was constructed for use in the field, anything in the nature of complications being impracticable. The apparatus consisted of a wide-mouthed thermos jar which contained a freezing mixture of salt and snow (with which a temperature of −22° C. could be reached, though such a figure was not by any means required). Into this projected two chambers in which the air was dried by $CaCl_2$ in lumps. In the air chambers were placed the individual insects to be experimented upon, each being enclosed in a small "cage" consisting of a piece of glass tubing with a gauze over the open end. This "cage" was attached at its other end to a thermometer whose bulb was arranged so that it was closely adjacent to the insect. The cage could be drawn up on its thermometer into an observation extension of the air chamber above the mouth of the jar. It was a simple matter to regulate the freezing mixture in such a way that the insect could be cooled down at any convenient rate, and

[1] *Ann. Mag. Nat. Hist.* (10), **14**, 204 (1934).

in its "cage" it could be drawn up at intervals for examination. By tapping the "cage" against the side of the chamber as a stimulus, it was possible to determine the degree of activity at any particular temperature. All the experiments were done in the dry in order not to have another variable factor, the humidity, changing at the same time.

During the cooling process the animals were in semi-darkness, so that their body temperatures could not have been above that of the air around them. Though a small dark-coloured body such as an insect would have a large surface area for the absorption of radiation relative to its bulk, it will at the same time have a large surface tending to keep it in equilibrium with, and to make it respond very rapidly to, changing air temperatures. In this way representatives of the main families of insects and various spiders were experimented upon, and it was found that two distinct and well-marked points could be determined, *A* and *B*; *A* being the point of cold rigor, below it the animal being inactive, above it slightly active, and *B* being the point below which it was judged that the insect could no longer retain its normal or effective activity.

After these experiments had been completed there came to the notice of the author a most comprehensive paper by Krogerus (**4**), in which are described in great detail certain investigations carried out upon the ecology of the animals living in the drifting sand dunes of Finland. In the course of his investigations, laboratory tests were made of the the influence exerted by certain isolated climatic factors (temperature, light, humidity, wind) upon the arthropods under examination (though realising that the climatic factors could be isolated only for convenience of manipulation). In his investigations upon the effect of temperature, experiments analogous to those done in East Greenland were carried out. Groups of 3–6 insects were enclosed in small "cages" in a chamber whose temperature was controlled. (An effort was made at the same time to control the humidity.) The insects were cooled until cold rigor had set in by exposure to a temperature of approximately zero° C. previous to the experiment proper. They were then gradually warmed at the rate of 1° C. in 2 min. and the temperature taken at certain well marked points, viz.:

(1) The first movement observed.
(2) All the animals active.
(3) All completely active.
(4) The first onset of heat paralysis.
(5) All heat paralysed.

Thus it is seen that Krogerus' figures are directly comparable with those for the Greenland arthropods, his points 1 (or more exactly the average of 1 and 2) and 3 corresponding to the points *A* and *B* in the Greenland experiments.

The Greenland data are set out pictorially together with that part of Krogerus' figures that applies, in Fig. 1, in which the percentage of insect

species having the point *A* or *B* at each temperature is plotted against degrees Centigrade.[1]

## 4. Summary and conclusions.

Independent investigations have now been made into the low temperature limit of activity of insects in East Greenland and Finland. From these it is clear that the insects of the Scoresby Sound region are much better equipped

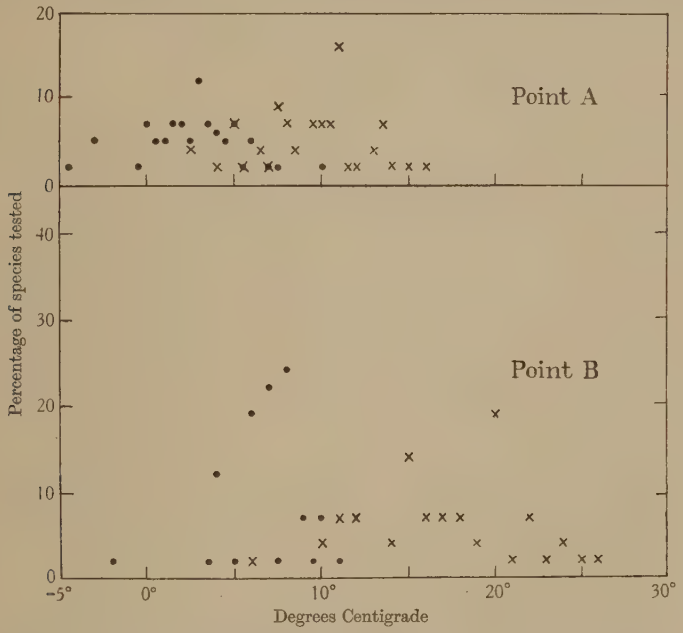



Fig. 1. Percentage of species tested with the point A or B per degree Centigrade.
Greenland • Finland ×

in their reactions for successful life under the prevailing low temperature conditions than would be those of Finland were they transported there. At 10° C. all but one of the East Greenland Arthropod fauna experimented upon have become fully active, while below that temperature none of the Finland insects has complete activity. A further possible "advantage" that the Greenland forms are seen to possess compared with those from Finland is that in the former there is a smaller average difference between

[1] In the appendix are set out the figures for each species experimented upon both in Finland and in Greenland, together with figures for certain Greenland spiders, whose ability to remain active at low temperatures is remarkable.

the lowest temperature at which any activity is possible and that at which complete activity is attained. Thus the average difference between these two points (*A* and *B*) for the Finland insects is 7·8° C., while that of those from East Greenland is only 4·1° C.

None of those species tested by Krogerus in Finland is the same as any of those experimented upon in Greenland, so that at present it is not known whether there exist different biological races of the same species possessing different adult reactions to low temperatures. Clearly, however, the East Greenland arthropods are better adapted for successful adult life under adverse temperature conditions than are those of Finland.

## APPENDIX.

### *Species of animals studied experimentally.*

| | Temp. (° C.) | | No. of individuals used |
|---|---|---|---|
| | *A* | *B* | |
| *Greenland insects.* | | | |
| HEMIPTERA. | | | |
| *Chlamydatus pulicarius* Fall. | 4·0 | 6·0 | 1 |
| TRICHOPTERA. | | | |
| *Apatania arctica* Boheman. | 1·5 | 3·5 | 2 |
| COLEOPTERA. | | | |
| *Coccinella transverso-guttata* Fald. | 5·0 | 9·0 | 1 |
| LEPIDOPTERA. | | | |
| *Sympistis zetterstedtii* Staudinger. | 3·0 | 8·0 | 3 |
| *Cidaria polata byssata* Aurivillius. | 6·0 | 7·5 | 2 |
| *Scoparia centuriella* Schiffermüller. | 4·0 | 7·0 | 1 |
| *Argynnis chariclea arctica* Zett. | 10·0 | 11·0 | 1 |
| DIPTERA. | | | |
| *Exechia frigida* Holmg. | 4·0 | 7·0 | 3 |
| *Rhymosia* sp.nov. | 1·0 | 6·0 | 1 |
| *Sciara* sp. | −4·5 | 5·0 | 1 |
| *Simulium* (*Prosimulium*) sp. cf. *ursinum* Edw. | 0·5 | 9·0 | 1 |
| *Aëdes? nigripes* Zett. | 6·0 | 8·0 | 1 |
| *Trichocera lutea* Becher. | 1·5 | 4·0 | 1 |
| *Orthocladius? conformis* Holmg. | 3·0 | 6·0 | 1 |
| *O.* sp. | 0·5 | 6·0 | 2 |
| *O.?* perennis | 2·0 | 7·0 | 1 |
| *Cricotopus basalis* Staeg. | 0 | 8·0 | 1 |
| *Smittia* sp. | 1·0 | 4·0 | 1 |
| *Rhamphomyia* sp. cf. *vesiculosa* | 3·5 | 7·0 | 2 |
| *R.* sp. | 0 | 4·0 | 1 |
| *R.* sp. | 2·5 | 8·0 | 1 |
| *Cynomyia mortuorum* L. | 0 | 6·0 | 3 |
| *Phormia? terraenovae* R. D. | 4·0 | 8·0 | 1 |
| *P.* sp. | 3·0 | 4·0 | 1 |
| HYMENOPTERA. | | | |
| *Bombus arcticus* K. | 5·0 | 9·5 | 3 |
| *Atractodes bicolor arcticus* Holmg. | 4·5 | 10·0 | 1 |
| *A. aterrimus* Holmg. | 2·0 | 8·0 | 1 |
| *Coelichneumon solutus occidentalis* Roman | 5·5 | 9·0 | 1 |
| *Homotropus groenlandicus* Holmg. | 4·5 | 8·0 | 1 |
| *Saotis hoeli* Roman. | 1·5 | 8·0 | 1 |

| | Temp. (° C.) A | Temp. (° C.) B | No. of individuals used |
|---|---|---|---|
| *Further Greenland diptera as yet not identified.* | | | |
| | −3·0 | 4·0 | |
| | 3·0 | 7·0 | |
| | 4·0 | 7·0 | |
| | 5·0 | 7·0 | |
| | 3·0 | 6·0 | |
| | 7·5 | 10·0 | |
| | −3·0 | −2·0 | |
| | 7·0 | 10·0 | |
| | 4·0 | 6·0 | |
| | 3·5 | 7·0 | |
| | −0·5 | 7·0 | |
| | 3·5 | 8·0 | |
| | 2·0 | 6·0 | |
| | 2·5 | 8·0 | |
| *Greenland spiders.* | | | |
| *Lycosa glacialis* Thor. | 0 | 3·0 | 4 |
| *Islandiana princeps* Braendegaard. | −3·0 | 3·0 | 1 |
| *Xysticus bimaculatus* Emerton. | 4·0 | 8·0 | 1 |
| *Dictyna borealis* Cambridge. | 0 | 2·0 | 1 |
| *Coryphaeolanus thulensis* Jackson. | −3·0 | 0 | 3 |
| *Finland insects.* | | | |
| ORTHOPTERA. | | | |
| *Gomphocerus aculatus* Thbg. | 8·0 | 20·0 | |
| *Sphingonotus coerulans* L.ssp. *intermedius* Ramme. | 5·5 | 21·0 | |
| HEMIPTERA. | | | |
| *Phimodera humeralis* Dalm. | 14·0 | 22·0 | |
| *Aphanus phoeniceus* Rossi. | 9·5 | 20·0 | |
| *Ischnodemus sabuleti* Fall. | 11·0 | 20·0 | |
| *Liburnia excisa* Mel. | 5·0 | 12·0 | |
| COLEOPTERA. | | | |
| *Cicindela maritima* Dej. | 15·0 | 25·0 | |
| *C. silvatica* L. | 13·0 | 24·0 | |
| *C. hybrida* L. | 10·5 | 24·0 | |
| *Dyschirius arenosus* Steph. | 7·0 | 11·0 | |
| *D. obscurus* Gyll. | 7·5 | 11·0 | |
| *Amara silvicola* Zimm. | 7·5 | 14·0 | |
| *Hesperophilus arenarius* Payk. | 6·5 | 10·0 | |
| *Negastr. pulchell?* | 8·5 | 20·0 | |
| *Paratinus femoralis* Er. | 6·5 | 12·0 | |
| *Notoxus monoceros* L. | 8·0 | 17·0 | |
| *Anthicus antherinus* L. | 8·0 | 15·0 | |
| *A. sellatus* Panz. | 5·0 | 12·0 | |
| *Eonius bimaculatus* Gyll. | 5·0 | 15·0 | |
| *Cneorrhinus plagiatus* Schall. | 11·0 | 17·0 | |
| *Aegialia arenarius* Fabr. | 11·0 | 16·0 | |
| LEPIDOPTERA. | | | |
| *Satyrus semele* L. | 11·0 | 15·0 | |
| *Arenostola elymi* Tr. | 4·0 | 10·0 | |
| *Crambus fascelinellus* Rb. | 2·5 | 11·0 | |
| *Pyrausta cingulata* L. | 10·0 | 16·0 | |
| *Scythris inspersella* Hb. | 7·5 | 15·0 | |
| *S. siccella* Zell. | 8·5 | 15·0 | |
| DIPTERA. | | | |
| *Aspistes berolinensis* Meig. | 7·5 | 15·0 | |
| *Philonicus albiceps* Meig. | 13·5 | 23·0 | |
| *Lasiopogon cinctus* Fabr. | 11·5 | 20·0 | |
| *Machimus atricapillus* Fall. | 10·5 | 19·0 | |
| *Laphria flava* L. | 13·0 | 22·0 | |
| *Thereva annulata* Fabr. | 10·0 | 20·0 | |
| *Chersodromia cursitans* Zett. | 11·0 | 20·0 | |
| *Tetanops myopina* Fall. | 11·0 | 16·0 | |
| *Oscinella albipalpis* Meig. | 9·5 | 14·0 | |
| *Paragusia elegantula* Zett. | 9·5 | 22·0 | |
| *Helina protuberans* Zett. | 10·0 | 18·0 | |
| *Hylemyia candens* Zett. | 11·0 | 19·0 | |

| | Temp. (° C.) | |
|---|---|---|
| | *A* | *B* |
| *Finland insects* (cont.) | | |
| HYMENOPTERA. | | |
| *Andrena argentata* Sm. | 16·0 | 26·0 |
| *Psammochares infuscatus* Lind. | 13·5 | 18·0 |
| *P. plumbeus* Fabr. | 13·5 | 17·0 |
| *P. fuscus* L. | 10·5 | 18·0 |
| *Mimesa inicolor* Lind. | 12·0 | 20·0 |
| *Artanes fallax* Sund. | 2·5 | 6·0 |

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# THE BREEDING BIRD POPULATION OF BRITISH HEATHS AND MOORLAND[1]

By DAVID LACK.

## TOGETHER WITH AN ACCOUNT OF A CENSUS OVER SEVEN YEARS ON SKOKHOLM, PEMBROKESHIRE

By R. M. LOCKLEY.

(*With* 1 *Figure in the Text*).

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## 1. Introduction.

As part of the scientific programme of the recently formed British Trust for Ornithology, an enquiry is being made into the factors affecting bird populations. Heathland is being specially studied, since it forms one of the simplest bird habitats in Britain. The present census figures are being published, though preliminary to the main enquiry, since very few figures are available for the density of the bird population in a comparatively uniform habitat. It will be yet some time before useful conclusions will have been attained as to the factors affecting the populations concerned.

I am indebted to the Scientific Committee of the Trust for the opportunity of undertaking this work, and to the following persons for helping to make the observations on which this paper is based: Messrs R. Blockey, K. Dixon, J. C. S. Ellis, R. M. Lockley, E. M. Nicholson, H. N. Southern, G. M. Spooner, J. F. Thomas, L. S. V. Venables; and members of the Cambridge Bird Club (results sent in by W. R. D. Harrisson and P. F. Holmes).

[1] Publication of the British Trust for Ornithology.

### 2. Localities and season selected.

Observers were found for most of the important regions of heath and moorland in England, together with one in Scotland and one in Ireland. They were asked to select an area if possible quite devoid of trees and bushes. Where possible heather (*Calluna*) heath was selected, but in some cases grass; in others a mixture of the two, and other elements also, were unavoidably included.

Only close observation throughout the breeding season can establish the full number of breeding pairs. Where, as in many cases, this could not be done, the time chosen for observation was as late as possible before the first young flew from the nest. This was to avoid confusing the young with breeding adults, while allowing time for all or nearly all the latter to have taken up their positions. In one case (Lundy) the counts had unavoidably to be taken when a few young had already left the nest, so that the figures for this area are rather too high. But most of the nests here still contained eggs or young and, especially since the season was apparently a late one, very few young were already so far advanced as to be difficult to distinguish from adults. The maximum possible error in the figures is thought to have been 10 per cent. It should be noted that 1934 was an exceptionally dry summer. Whether this affects the density of the breeding population on heathland is not known; but at any rate the Skokholm figures for 1934 do not differ greatly from those of previous years.

### 3. Census methods.

(*a*) *Nests.* The only accurate method is to find all the nests in the area concerned and to observe carefully any resident non-breeding birds. As well as giving a figure for the population density, this method allows of observations on territory, the non-breeding population and other problems, which cannot be investigated by the other methods to be described. It is also much the most satisfactory where comparison is desired over a period of years. But it takes up more time than many observers can afford, and is impracticable if the sole fact required is the population density, since the necessarily small area selected may not be typical of the region.

(*b*) *Observation.* By this is meant repeated observation in an area to determine the exact number of resident adult birds but without finding their nests. It has the advantage over the nest method of saving time, but does not differentiate breeding from non-breeding adult birds. As in the nest method, the small area selected may not be typical of the region.

(*c*) *Rope method.* A rope (binder-twine is best), preferably 48 yards long, is held taut, and the observers move at right angles to it across the region selected. The distance traversed is best measured from a map, as on Lundy, but if this is impracticable, two or more observers walk steadily, counting the number of paces taken. The length of stride under these conditions is tested. The area covered is readily calculated. All birds which rise between the two

outside observers are counted. Under the conditions met it was always possible to avoid counting in again any birds which flew up and settled ahead, but this became very difficult where the average density over a long stretch was higher than two birds to the acre. With a rope 48 yd. long, four observers equally spaced along it was found to be the best number. With only three observers, a few birds tended to let the rope pass over them without rising, and so were liable to be overlooked. With this number, a smaller length of rope is more satisfactory. The method is practicable only in the very open types of vegetation such as are found on heaths, and would be useless in bushy areas with skulking birds.

Provided a sufficiently long stretch is taken, it is reasonable to assume that the number of birds met in the sample strip is proportional to their density in the region concerned. Since 150 acres can readily be counted in one day, a much greater area can be covered than by either of the first two methods, where about 100 acres is the most that the average observer has time to watch accurately in one season. Also, since long strips are taken, the sample is likely to be more representative than a sample square area, which is the best shape for the first two methods. I consider the rope method much the best to use if the sole fact required is an estimate of the density of the summer population. In the counts, each adult bird is recorded, and no distinction can be made between breeding and non-breeding adults.

(*d*) *Walking.* A number of observers walk in line, working the selected area in strips until the whole has been covered. The chief source of error is from birds which are put up and fly out to the side into a part of the area not yet counted. Both skylark and meadow pipit (the two commonest heath birds) are very wide-ranging and readily fly into each others' territories. With a density of over 50 birds per 100 acres, it is extremely difficult to check up on these birds. This method is much the quickest of those mentioned, but is much the most liable to error, and can be usefully employed only in order to get a rough idea of the density in areas with a comparatively sparse population.

On Dartmoor an area of 49 acres, roughly square in shape, was walked on three occasions in May, being covered in from six to eight adjacent strips. The skylarks recorded varied between 6 and 10, the meadow pipits between 14 and 18. This gives a maximum of 28 birds, a minimum of 20 (the average of these was taken for the figure in the table). With a higher density of birds, the degree of possible error increases considerably over this.

On Lundy, the walking method was compared with the rope method. The two counts are in close agreement, but the figures are too few for importance to be attached to them.

Area 1. By walking: 10 adults on 18 acres (55 birds per 100 acres).
By rope sample: 4 adults on 8 acres (50 birds per 100 acres).

Area 2. By walking: 157 adults on 70 acres (224 birds per 100 acres).
By rope sample: 17 adults on 8 acres (212 birds per 100 acres).

Table 1. *Counts on heaths and moorland taken in* 1934.

| Locality | Method (*Observer*) | Area in acres | No. of adult birds | Adults per 100 acres |
|---|---|---|---|---|
| 1. Seaford Downs, Sussex, 150–400;* very short grass turf | Nests (*J. F. Thomas*) | 60 | 2 | 3 |
| 2. Dartington meadowland, S. Devon, 200; grass | Observation (*D. Lack*) | 106 | 7 | 7 |
| 3. Brow Grains moor, Yorks., below 1000; grass, heather, bracken, bog | Nests (*J. C. S. Ellis*) | 100 | 22 | 22 |
| 4. Studland Heath, Dorset, sea-level; heather, some marram grass | Nests (*G. M. Spooner*) | 63 | 14 | 22 |
| 5. Frensham heath, Surrey, 200; dry heather | Nests (*L. S. V. Venables*) | 100 | 32 | 32 |
| 6. Blackdown heath, Surrey, 900; dry heather | Rope (*R. Blockey, L. S. V. Venables*) | 10 | 4 | 40 |
| 7. Seaford Downs, Sussex, 400–500; long grass | Nests (*J. F. Thomas*) | 33 | 14 | 42 |
| 8. Stoneycross, New Forest, 200; heather, some grass | Rope (*R. Blockey, H. N. Southern, L. S. V. Venables*) | 92 | 48 | 52 |
| 9. Letterfrack, W. Galway, 250; grass, heather, cotton grass | Walk (*E. M. Nicholson*) | 50 | 28 | 56 |
| 10. South Downs, nr. Petersfield, Hampshire, *c.* 800; grass | Rope (*L. S. V. Venables*) | 40 | 24 | 60 |
| 11. Mainland, Shetland Is., 0–200; heather and grass | Rope (*H. N. Southern, L. S. V. Venables*) | 75 | 52 | 69 |
| 12. Breckland, Suffolk, Norfolk, below 200; heather and grass | Rope (*W. R. D. Harrisson, P. F. Holmes*) | 65 | 46 | 71 |
| 13. Skokholm, Pembroke, 100; heather, bracken, grass, bog | Observation (*R. M. Lockley*) | 220 | 224 | 102 |
| 14. Sleights Moor, Yorkshire, 400–800; mainly heather, some grass and whortleberry | Nests (*K. Dixon*) | 144 | 218 | 151 |
| Same, excluding red grouse, which is specially protected | ,, | 144 | 136 | 94 |
| 15. Dartmoor, S. Devon, 1000–1500: | (*D. Lack, G. M. Spooner, L. S. V. Venables*) | 326 | 176 | 54 |
| (*a*) very bare top of moor, Plym Head | Rope | 57 | 7 | 12 |
| (*b*) average top of moor, Buckfastleigh, Lee Moor | Rope | 132 | 58 | 44 |
| (*c*) open heather, Rippon Tor | Walk (repeated) | 49 | 24 | 48 |
| (*d*) thicker vegetation on open moor, Buckfastleigh, Lee Moor | Rope | 44 | 41 | 93 |
| (*e*) edge of moor, near cultivation, Buckfastleigh | Rope | 35 | 33 | 94 |
| (*f*) marsh and bog (grass, heather, cotton grass, *Juncus*), Lee Moor | Rope | 9 | 13 | 144 |
| 16. Lundy, N. Devon, 200–400; grass, heather, bracken | (*D. Lack*) | 276 | 344 | 125 |
| (*a*) Northern quarter: | | | | |
| (1) burnt northern end | Walk | 36 | 0 | 0 |
| (2) more northern part | Walk | 52 | 10 | 19 |
| (3) southern part | Walk | 54 | 64 | 119 |
| (*b*) Three-quarter section: | Walk | 88 | 167 | 190 |
| Thicker vegetation here | Walk | 70 | 157 | 224 |
| (*c*) Rope samples over island: | | | | |
| (1) bare areas with very short vegetation | Rope | 16 | 4 | 25 |
| (2) thicker vegetation | Rope | 66 | 86 | 130 |

* Altitude in feet above sea-level.

Table 2. *Summary of the species found.*

| Name of species | Number of adults found in area no. | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| Carrion crow<br>*Corvus corone corone* | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . |
| Hooded crow<br>*Corvus cornix cornix* | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . |
| Shetland starling<br>*Sturnus vulgaris zetlandicus* | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . |
| Twite<br>*Carduelis f. flavirostris* | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 6 | . | . |
| Linnet<br>*Carduelis c. cannabina* | . | . | . | . | 2 | . | 2 | 6 | . | . | . | 1 | . | . | . | . |
| Chaffinch<br>*Fringilla c. coelebs* | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . |
| Yellow bunting<br>*Emberiza c. citrinella* | . | . | . | . | . | . | . | . | . | 3 | . | . | . | . | . | . |
| Reed bunting<br>*Emberiza s. schoeniclus* | . | . | . | . | 2 | . | . | . | . | . | . | . | . | 8 | . | . |
| Woodlark<br>*Lullula a. arborea* | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . |
| Skylark<br>*Alauda a. arvensis* | . | 5 | 2 | . | 2 | . | 4 | 15 | 22 | 16 | 13 | 17 | 6 | 6 | 78 | 47 |
| Tree pipit<br>*Anthus t. trivialis* | . | . | . | . | 4 | 1 | . | . | . | . | . | . | . | . | . | . |
| Meadow pipit<br>*Anthus pratensis* | . | . | 7 | 14 | 14 | . | 6 | 24 | 4 | 1 | 17 | 17 | 82 | 62 | 94 | 293 |
| Whitethroat<br>*Sylvia c. communis* | . | . | . | . | . | 3 | . | . | . | . | . | . | . | . | . | . |
| Dartford warbler<br>*Sylvia undata dartfordiensis* | . | . | . | . | 4 | . | . | . | . | . | . | . | . | . | . | . |
| Song thrush<br>*Turdus e. ericetorum* | . | . | . | . | . | . | . | . | . | . | . | . | . | 4 | . | . |
| Blackbird<br>*Turdus m. merula* | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . |
| Ring ousel<br>*Turdus t. torquatus* | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . |
| Wheatear<br>*Oenanthe oe. oenanthe* | 2 | . | . | . | . | . | . | . | . | . | 4 | 7 | 28 | 4 | . | . |
| Whinchat<br>*Saxicola r. rubetra* | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . |
| Stonechat<br>*Saxicola torquata hibernans* | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 1 | . |
| Dunnock or hedge-sparrow<br>*Prunella modularis occidentalis* | . | . | 2 | . | . | . | . | . | . | . | . | . | 14 | . | . | . |
| Wren<br>*Troglodytes t. troglodytes* | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . |
| Cuckoo<br>*Cuculus c. canorus* | . | . | . | . | . | . | . | . | . | 3 | . | . | . | . | 1 | . |
| Little owl<br>*Asio otus wilsonianus* | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . |
| Merlin<br>*Falco columbarius aesalon* | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . |
| Mallard<br>*Anas p. platyrhyncha* | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . |
| Teal<br>*Anas c. crecca* | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | 1 |
| Stone curlew<br>*Burhinus oe. oedicnemus* | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Ringed plover<br>*Charadrius h. hiaticula* | . | . | . | . | . | . | . | . | . | . | 8 | . | . | . | . | . |
| Golden plover<br>*Charadrius a. apricarius* | . | . | . | . | . | . | . | . | 2 | . | 2 | . | . | 15 | . | . |
| Lapwing<br>*Vanellus vanellus* | . | . | . | . | . | . | . | 1 | . | . | . | . | 16 | 18 | . | 2 |

Table 2 (*cont.*).

| Name of species | Number of adults found in area no. | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| Oyster-catcher | | | | | | | | | | | | | | | | |
| *Haematopus ostralegus occidentalis* | . | . | . | . | . | . | . | . | . | . | . | . | 70 | . | . | . |
| Dunlin | | | | | | | | | | | | | | | | |
| *Calidris alpina schinzii* | . | . | . | . | . | . | . | . | . | . | . | . | . | 3 | . | . |
| Curlew | | | | | | | | | | | | | | | | |
| *Numenius a. arquata* | . | . | 4 | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Common snipe | | | | | | | | | | | | | | | | |
| *Capella g. gallinago* | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | 2 | . |
| Moorhen | | | | | | | | | | | | | | | | |
| *Gallinula c. chloropus* | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . |
| Pheasant | | | | | | | | | | | | | | | | |
| *Phasianus colchicus* | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | 1 |
| Common partridge | | | | | | | | | | | | | | | | |
| *Perdix p. perdix* | . | 2 | . | . | . | . | 2 | . | . | 1 | . | . | . | . | . | . |
| Red-legged partridge | | | | | | | | | | | | | | | | |
| *Alectoris r. rufa* | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Red grouse | | | | | | | | | | | | | | | | |
| *Lagopus s. scoticus* | . | . | 7 | . | . | . | . | . | . | . | . | . | . | 82 | . | . |

## 4. Population density.

As a result of the enquiry, a number of figures are now available for the density of the breeding population on British heaths and moorland, with a few on downs and grassland for comparison. From 20 to 100 adults per 100 acres were the most usual figures, but some were considerably below, others considerably above, these figures, the minimum being 3, the maximum about 224 adults per 100 acres. (The latter is perhaps a little too high since a few young had left the nest and may have been included as adults.) Many bird censuses have been taken, but few have been restricted to one type of habitat, and none of the latter concern British heathland. In 1930 V. C. Wynne Edwards and T. H. Harrisson (**3**) made a breeding census of Lundy by walking, and in 1931 T. H. Harrisson and D. Lack (**1**) made a census by the same method on St Kilda. Both these included a large stretch of cliff, also some houses and cultivated land, and hence cannot be compared with the present results.

## 5. Habitat variation.

Heathland was chosen as being the simplest habitat in Britain. But even where trees and bushes were omitted, the variations in habitat within the term "heath" proved extremely large. These variations were correlated partly with differences in the composition of the vegetation (ling, heather, grass, bracken, whortleberry, etc.) and partly with differences in its height (connected with the degree of exposure, water supply, grazing, etc.). Also in some areas there were rock outcrops, in others a few bushes had unavoidably to be included. Owing to this variation, it proved impossible to find any area of heath which might be described as "uniform", even over a few square yards. These varia-

tions in vegetation were associated with very marked differences in the bird population density, even in closely adjoining areas. On open moorland on Dartmoor the average density varied between 12 and 94 adults per 100 acres. Here the vegetation was mainly of a similar nature, and it was chiefly its height which varied. On Lundy, where the vegetation differed more in specific composition, the variation in density was considerably greater, from 19 to 224 adults per 100 acres.

No particular area of heathland in any region could be termed typical of that region. Nor, between the wide limits already mentioned, can any particular density of birds be considered typical for British heathland. It follows that figures for the breeding density of birds in an area mean almost nothing without an extremely detailed description of the significant features in the area concerned, and this is considerably complicated by the fact that these significant features often vary greatly within the space of ground occupied by one breeding pair. This consideration does not appear to have been taken account of in other censuses, though it applies with much more force to areas which include bushes and trees than it does to heathland, especially where the habitat is of a mixed nature, such as, for instance, might come under the term "agricultural land".

### 6. Geographical variation.

Rather different species inhabit different heaths in England and Scotland (some details of this are apparent from Table 2). It was hoped that differences in the total population density might be revealed by the present enquiry, but any such differences were completely obscured by the habitat variation already discussed. It seems impossible to find two heathland areas sufficiently similar to make a significant comparison between different geographical regions.

### 7. Non-breeding population.

Only the nest method, supported by careful observations, gives data on the non-breeding population. The term "non-breeding" is here used for residents, but not for passing migrants, and is not extended to those birds feeding in the area and breeding outside it, of which there were a few in some of the areas. Passage migrants and the latter group are omitted entirely from the counts. At Frensham L. S. V. Venables found no non-breeding birds among 16 breeding pairs on 100 acres. Near by, he found a few non-breeding curlew near the breeding pairs. In Yorkshire J. C. S. Ellis found on 100 acres 7 breeding pairs (1 of skylark, 3 of meadow pipit, 1 of dunnock, 2 of red grouse) and 8 non-breeding individuals (1 meadow pipit, 4 curlew, 3 red grouse). This is a high percentage. The only non-breeding individuals reported by K. Dixon on 144 acres, also in Yorkshire, were a single golden plover and a single dunlin, out of 218 adults. On Lundy, no special look-out was kept; five non-breeding curlew were present, but not on the census area itself.

These non-breeding individuals have been omitted from Table 1, but, where they occurred in the census area, have been included in Table 2. It must

be noted that the rope method and the walking method do not differentiate breeding from non-breeding individuals, but the chief non-breeding individuals belong to the larger species, not to the small Passerines, and these larger birds occur very rarely in any of the rope counts. For a further discussion of non-breeding see Lockley's note. The latter studied the problem more fully than other observers.

### 8. Winter population.

The enquiry is primarily concerned with the density of the breeding birds. Four observers noted the winter population in the same areas which they had studied in summer, and these have been included for comparison with the summer figures already given. It must be borne in mind that the winter population in most areas of the type studied is liable to marked, and often sudden, fluctuations.

1. *Seaford Downs* (J. F. Thomas), 60 acres.
   15. 11. 34: 8 rooks (*Corvus f. frugilegus*),[1] 6 lapwing.
   25. 11. 34: 2 carrion crow.
   3. 12. 34: 1 kestrel (*Falco t. tinnunculus*).
   10. 12. 34: 2 carrion crow, 8 magpie (*Pica p. pica*), 8 partridge.
   *Total*: from 1 to 18 birds (Mr Thomas added that in some previous winters the total had at times greatly exceeded 18 birds).

3. *Brow Grains Moor* (J. C. S. Ellis), 100 acres.
   20. 11. 34: 40–50 red grouse. No other birds, but the remains of a chaffinch indicated a bird of prey.

7. *Seaford Downs* (J. F. Thomas), 33 acres.
   18. 11. 34: 4 skylark, 2 meadow pipits, 1 kestrel.
   21. 11. 34: 5 skylark, 5 meadow pipits, 1 green woodpecker (*Picus viridis virescens*).
   25. 11. 34: 7 skylark, 5 meadow pipits.
   28. 11. 34: 4 skylark, 2 meadow pipits, 4 partridge.
   9. 12. 34: 6 skylark, 2 meadow pipits.
   *Total* from 7 to 12 birds.

15*c*. *Dartmoor, Rippon Tor* (D. Lack), 49 acres.
   9. 12. 34: 10 meadow pipits.

Further winter figures will be found in the Appendix by R. M. Lockley. When the above figures are compared with those in Table 1, it is seen that the winter population on the first type of Seaford Downs and on Brow Grains Moor is higher than that of the breeding adults, as also is that on Skokholm. But the second Seaford Downs area and Rippon Tor have a lower winter than summer population.

### 9. Comparison with other regions.

Most censuses taken in England have referred either to farmland or to woods. These have shown without exception a considerably higher density than the heath and moorland figures here recorded. Perhaps of greater interest are the counts over heath and moorland in other parts of the world, but unfortunately very few are available. E. M. and B. D. Nicholson (Longstaff, **2**) found some 27 adults per 100 acres on about 5330 acres of tundra in West

[1] Latin names are included only where a species was not given in Table 2. In all cases they follow the British Check-List.

Greenland. But in the Arctic, as in England, there are very great local variations. The Nicholsons noted that in their census area the birds were mainly on the lower ground. On Bear Island in 1932 on tundra about 100 ft. above sea-level G. C. L. Bertram and I found no land birds at all on 4 sq. miles near the west coast. Here insect food was abundant, but the limestone afforded no crevices suitable for the nests of the snow bunting, *Plectrophenax nivalis* (L.). The densest population of land birds on this barren island was round the deserted village in the north-east, where about 3·2 adults per 100 acres were found on about 300 acres.

For the Tropics I obtained a very few rough figures in Tanganyika in August and September 1934. In a sheltered grassy valley with arborescent *Senecios* on Kilimanjaro at 12,000 ft., 10 acres supported a population of some 80–100 adults per 100 acres. But at this altitude the exposed heather-covered moorland supported a considerably lower population than that on Dartmoor at 1000 ft. (probably well below 20 adults per 100 acres), although the vegetation was considerably thicker and taller than on Dartmoor. On the Ngomeni savannah near Muheza at 700 ft.—an area covered with grass about a foot high with a few thorn bushes—a rope census of 11½ acres with Mr and Mrs R. E. Moreau gave a density of 96 adults per 100 acres. The density in the rather taller grass on the Monga downs above Amani at 3000 ft. was considerably lower than this, probably below 20 adults per 100 acres. On the other hand, some of the tall (6–12 ft. high) grassland between Muheza and Amani supported a very high population indeed. Three acres that I counted here had about 40 breeding adults to the acre, a far higher figure than I have counted in any other area. Though they were nesting there, not all of these birds derived the whole of their food supply from this area. It is to be hoped that further data will be obtained for tropical regions, as the above figures are based on very small areas.

## 10. Summary.

1. Preliminary to an enquiry into the factors regulating the bird population on British heaths and moorland, censuses of the breeding population were taken over approximately 1700 acres in various parts of England, Scotland and Ireland.

2. From 20 to 100 adults per 100 acres were the most usual figures for the breeding density in this habitat, the minimum being 3 and the maximum about 224 adults per 100 acres.

3. The variations in density in the same region due to differences in the height and quality of the vegetation were extremely large, and made it impossible to measure geographical variations.

## REFERENCES.

(1) **Harrisson, T. H. and Lack, D. (1934).** "The breeding birds of St Kilda." Scot. Nat. 59–69.

(2) **Longstaff, T. G. (1932).** "An ecological reconnaissance in West Greenland." J. Anim. Ecol. 1, 119.

(3) **Wynne-Edwards, V. C. and Harrisson, T. H. (1934).** "A bird census on Lundy Island (1930)." J. Ecol. 20, 371–9.

# APPENDIX

## A CENSUS OVER SEVEN YEARS, ON SKOKHOLM, PEMBROKESHIRE

By R. M. LOCKLEY.

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### 1. Introduction.

It is not intended to give here an elaborate analysis of the results obtained over the years 1927–34 of census work on the island of Skokholm. I shall hope to accomplish this at some later date. For the moment it will suffice to give as much as can be economically collated with the census figures for heathland areas as tabulated above by D. Lack.

Skokholm is an island off the Pembrokeshire coast, in area less than 250 acres and rising in the form of a rough plateau averaging about 100 ft. above sea-level. It is covered with closely grazed turf which comprises about 45 per cent. of the whole, bracken 30 per cent., coarse bog grass 15 per cent. and heather 10 per cent. At intervals there are rocky outcrops rising a few feet above the surface and covered with lichen and stunted heather. Here, during a residence begun in 1927 and continued intermittently to the present day, census work has been carried out at various dates in every month of the year. It is, however, outside the scope of this paper to make any but a few general remarks on method and conclusions, and to give the tabulated results of a census, taken in June each year, of the strictly heathland breeding species.

### 2. Definition of heathland birds.

It is necessary to arrive at, and abide by, a definition as to what constitutes, for the purpose of this paper, a heathland breeding species. Obviously a true heathland bird is one which feeds and breeds exclusively on a heathland area without having to resort to nearby cover (crags, cliffs or trees) for food or shelter, or to build its nest. This definition has been used to determine which of the 30 odd species which breed on Skokholm may be considered heathland species. It will be seen that 16 species passed the test, including some of the carrion crows which nested inland on the rock outcrops. The rest

of the carrion crows, ravens, choughs, peregrine falcons, pied wagtails, swallows, etc., though they fed over the heathland, are not included, since they nested (and partly fed in some cases) on parts of the island which could not be classed as heathland.

### 3. Method.

The greater part of the island was "walked" every day from late March to the end of June in the performance of other duties (shepherding, etc.), so that most of the small breeding birds were known individually by their constant appearance at certain places or "territories". In many cases their nests were found, and these, together with the whereabouts of nests suspected, but for lack of time not found, were marked on a large-scale map. The plotting of these was made easy by the fact that the island is divided up into sections or fields by (now tumble-down) stone and earth hedges, while the rock outcrops are further useful topographical points. As many breeding pairs as possible having been plotted, in addition I devoted one or more days early in June wholly to the checking up and filling in of gaps in the midsummer census of breeding birds. This was accomplished by walking up and down each field or section so as to cover the whole of the ground, beating vegetation to left and right with a willow rod. A few young birds—wheatears, meadow pipits, hedge-sparrows —might be on the wing in early June, but as I was, from earlier daily walks, already familiar with these fledgelings, I was able to make allowance accordingly.

### 4. Non-breeding population.

Of apparently non-breeding birds among the Passerine species very few were seen and none regularly in any one spot. But among the waders and ducks and quite apart from passage migrants and casual visitors, which are not considered here, there were often resident at midsummer large flocks of non-breeding curlews, lapwings, an occasional whimbrel, dunlin, or sandpiper, and mallard (chiefly drakes, sometimes a pair, or a single duck). These might be flushed anywhere on the island, for they by no means fed always by the ponds or damp places but often far enough out among heather and pasture to justify their being given status as true heathland non-breeding species. Nevertheless, it is impossible satisfactorily to attempt to include these non-breeding heathland species in my table, and in my opinion they should everywhere be dealt with quite separately, as has been suggested in regard to non-breeding birds in a recent Gannet Census (Salmon and Lockley (**1**)): impossible because the numbers of non-breeders will be found, by regular observation, to be very unstable. For instance, on Skokholm there might be resident for the first half of June 50 curlew and 20 mallard, and for the latter half 2 or less of each species. The casual observer spending one week on the island therefore would be misled as to the average numbers of the temporarily resident non-breeders. Dealt with separately, however, the figures for breeders and non-breeders

have their fullest value, and the latter especially for research in the future. Our present knowledge of the proportion of sexes and number of non-breeders attached to breeding pairs or groups is very slender, and as far as Skokholm is concerned the only species where this number is fairly constant throughout a season, and therefore readily ascertainable, is the oyster-catcher. This bird, by the way, is a true heathland species during the breeding season on Skokholm, three-fourths of the total numbers of breeding pairs breeding and feeding as exclusively on heathland as any stone curlew on the Breckland or curlew on an upland moor. I therefore include this proportion (three-fourths) in my census of heathland breeding species.

The figures given in Table 1 are therefore of breeding pairs only.

### 5. Relations with non-heathland species.

Just as, for example, a Surrey heath is liable to the incursion of woodland and meadowland species from the different types of country surrounding it, so the heathy surface of an island in the sea is often exposed to the incursion of maritime and pelagic species seeking a place to rear their young. Apart from the terrestrial species given in the table, Skokholm is occupied in summer by tens of thousands of gulls, auks, and petrels, which breed, not only along the coastal acres but also upon every inland acre of the island. In spite of this immense incursion of oceanic species the number of heathland breeders (even if for the moment we do not include the oyster-catchers) is well up to the average shown in Lack's tables. It may therefore be assumed that the presence on a heath of large numbers of birds which obtain their food from the sea, leaving the fauna and flora practically untouched, has no direct influence on the numbers of heathland feeding and breeding birds. The island of Grassholm may be cited as an example of a heath (20 acres, grass) where the numbers of the sea birds have been so great as to destroy some three acres of grass by community nesting and guano (gannet), and to destroy and alter the greater part of the grassy area by burrowing, undermining, and draining (puffin). There were no heathland breeding species on Grassholm in 1934.

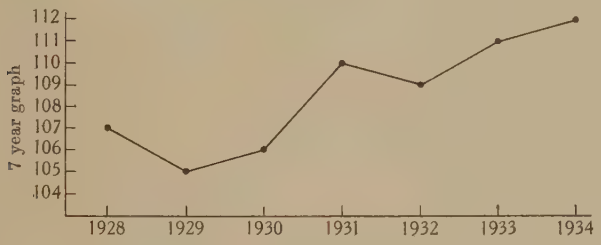
It should be explained that much of the grass and rock-strewn cliff slopes surrounding Skokholm also has been undermined by burrowing puffins and shearwaters, and the vegetation destroyed or altered, but that, since this rocky part cannot be classed as heathland, I have deducted its estimated area—some 20 odd acres—from the total acreage of the island, leaving a maximum heathland area of 220 acres.

### 6. Results of summer censuses.

The totals for each year have been remarkably stable, the variation at greatest not exceeding about 6 per cent. For the moment there is little obvious significance to be attached to the slight increase which the figures show over the seven years. This increase might possibly have been greater if

Table 1. *Summer breeding population of heathland species, Skokholm.*

| | 1928 | 1929 | 1930 | 1931 | 1932 | 1933 | 1934 | Average no. of birds |
|---|---|---|---|---|---|---|---|---|
| Carrion crow, *Corvus c. corone* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| Linnet, *Carduelis c. cannabina* | . | 1 | . | . | . | . | . | . |
| Skylark, *Alauda arvensis* | 3 | 3 | 2 | 4 | 3 | 3 | 3 | 6 |
| Meadow pipit, *Anthus pratensis* | 45 | 39 | 41 | 44 | 39 | 43 | 41 | 82 |
| Sedge warbler, *Acrocephalus schoenoboenus* | 1 | 1 | 1 | . | . | . | . | 1 |
| Whitethroat, *Sylvia c. communis* | . | . | . | 1 | 1 | . | . | <1 |
| Blackbird, *Turdus m. merula* | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 |
| Wheatear, *Oenanthe oe. oenanthe* | 10 | 13 | 12 | 9 | 13 | 13 | 14 | 24 |
| Stonechat, *Saxicola torquata hibernans* | 1 | . | . | . | 1 | . | . | <1 |
| Hedge-sparrow, *Prunella modularis occidentalis* | 5 | 6 | 5 | 6 | 7 | 6 | 7 | 12 |
| Little owl, *Athene noctua vidalii* | 1 | . | 1 | . | . | 1 | 1 | 1 |
| Oyster-catcher, *Haematopus ostralegus occidentalis* | 30 | 30 | 30 | 30 | 30 | 32 | 35 | 62 |
| Lapwing, *Vanellus vanellus* | 6 | 8 | 10 | 11 | 12 | 10 | 8 | 18 |
| Land rail, *Crex c. crex* | . | . | 1 | . | . | . | . | <1 |
| Water rail, *Rallus a. aquaticus* | . | 1 | . | 1 | . | . | . | <1 |
| Moorhen, *Gallinula c. chloropus* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| Total pairs | 107 | 105 | 106 | 110 | 109 | 111 | 112 | |




Highest total: 224 adults in 1934
Lowest „ 210 „ 1929
Average number of adults: 217
„ „ „ per 100 acres: 99
Number of adults per 100 acres in 1934: 102

certain factors, including the introduction of sheep, had not tended to reduce the amount of vegetation available for the use of cover nesting species—sedge warbler, whitethroat, blackbird, and stonechat; but it is too early yet to be definite on this point. The removal of the sheep in 1934 may result in a change in the heathland breeding population in 1935 and subsequently, following the increase in the luxuriance of the vegetation.

If one may judge from other census figures of 1934 given by Lack, Skokholm shows a high heathland breeding population for an exposed area swept by strong winds, and it may be supposed that the average of 51 pairs (102 adults) to 100 acres for 1934 is somewhere near the "climax" state consistent with this mixed type of heathland. The stability of the more numerous species, such as meadow pipit, wheatear, hedge-sparrow, and oyster-catcher, is of considerable interest, influencing greatly as it does the stability of the total population. It is quite possible that this stability is ensured more easily on an island than on a mainland heath because any gaps in the territories of the

regular breeders are more rapidly filled from the ranks of the great numbers of migrants which pass through the island in spring and autumn.

## 7. Winter counts.

Table 2 gives some specimen counts of the December bird population on Skokholm, for comparison with the winter figures for other areas given earlier. At this season, day to day variation is great, depending on the meteorological conditions. Those species whose numbers could not be accurately ascertained are marked with a "?".

Table 2. *Some specimen winter counts on Skokholm.*

| | 17 Dec. 1927 | 17 Dec. 1928 | 17 Dec. 1929 | 17 Dec. 1930 | 5 Dec. 1931 | 4 Dec. 1932 |
|---|---|---|---|---|---|---|
| Raven, *Corvus c. corax* | 2 | 2 | 2 | 2 | 2 | 2 |
| Carrion crow, *Corvus c. corone* | 3 | 6 | 4 | 1 | 4 | 3 |
| Chough, *Pyrrhocorax pyrrhocorax* | 1 | 4 | 9 | 2 | 2 | 2 |
| Starling, *Sturnus v. vulgaris* | 40 | 200 | 60 | 150 | 35 | 50 |
| Greenfinch, *Chloris c. chloris* | 1 | 3 | . | . | 6 | . |
| Goldfinch, *Carduelis c. britannica* | . | . | 5 | 1 | . | 1 |
| Linnet, *Carduelis c. cannabina* | . | . | 30 | 7 | . | . |
| Chaffinch, *Fringilla c. coelebs* | 4 | 4 | . | 1 | 2 | 2 |
| Skylark, *Alauda a. arvensis* | 8 | 4 | 12 | 21 | 3 | . |
| Meadow pipit, *Anthus pratensis* | 6 | . | 1 | . | 2 | 3 |
| Rock pipit, *Anthus spinoletta petrosus* | 12 | 9 | 5 | 20 | 2 | 10 |
| Pied wagtail, *Motacilla alba yarrellii* | 1 | . | . | . | . | . |
| Fieldfare, *Turdus pilaris* | . | 12 | . | 5 | . | 12 |
| Mistle thrush, *Turdus v. viscivorus* | . | . | 1 | . | . | . |
| Song thrush, *Turdus e. ericetorum* | 30 | 50 | 25 | 30 | 40 | 25 |
| Redwing, *Turdus m. musicus* | 3 | 1 | 2 | 12 | . | 9 |
| Blackbird, *Turdus m. merula* | 15 | 3 | 50 | 8 | 10 | 10 |
| Stonechat, *Saxicola torquata hibernans* | 3 | 4 | 2 | 1 | 2 | 1 |
| Robin, *Erithacus rubecula melophilus* | 3 | 4 | 1 | 1 | 5 | 4 |
| Hedge-sparrow, *Prunella modularis occidentalis* | 11 | 10 | 4 | 8 | 17 | 20 |
| Wren, *Troglodytes t. troglodytes* | 20? | 20? | 20? | 20? | 20? | 20? |
| Little owl, *Athene noctua vidalii* | 2 | 5 | 3 | 6 | 3 | 5 |
| Short-eared owl, *Asio f. flammeus* | . | . | . | . | . | 1 |
| Peregrine falcon, *Falco p. peregrinus* | 1 | 2 | . | 1 | . | . |
| Kestrel, *Falco t. tinnunculus* | 1 | . | 1 | . | 1 | 1 |
| Common buzzard, *Buteo b. buteo* | 2 | 2 | 1 | 2 | 2 | 2 |
| Mallard, *Anas p. platyrhyncha* | 30 | 20 | 40 | 30 | 60 | 80 |
| Teal, *Anas c. crecca* | 10 | 6 | 12 | 9 | 20 | 10 |
| Wigeon, *Anas penelope* | 50? | 50? | 60? | 5? | 20? | ? |
| Golden plover, *Charadrius apricarius* | 1 | . | . | . | . | . |
| Lapwing, *Vanellus vanellus* | 150 | 60 | 30 | 80 | 100 | 150 |
| Curlew, *Numenius a. arquata* | 40 | 5 | 12 | 1 | 12 | . |
| Common snipe, *Capella g. gallinago* | 30 | 60 | 40 | 50 | 5 | 12 |
| Jack snipe, *Lymnocryptes minimus* | 5 | 1 | . | 3 | . | . |
| Woodcock, *Scolopax r. rusticola* | 1 | 20 | 2 | . | 1 | . |
| Water rail, *Rallus a. aquaticus* | 15? | 15? | 15? | 15? | 20? | 15? |
| Total | 501 | 582 | 449 | 492 | 396 | 450 |

Largest total = 582, smallest total = 396, average total = 478.

## 8. Summary.

1. A yearly census for seven years of regular inhabitants of heathland on Skokholm, an island off the coast of Pembrokeshire, South Wales, is described.

2. The definition of a heathland species is discussed.

3. On Skokholm the oyster-catcher is a regular heathland species in the breeding season.

4. The numbers of heathland breeding birds have remained fairly constant from 1928 to 1934 (the greatest variation being about 6 per cent.). There was a slight trend of increase over the seven years.

5. The average density was about 99 adults per 100 acres. The most numerous species were meadow pipit, oyster-catcher, wheatear, hedge-sparrow, and lapwing.

REFERENCE.

(1) **Salmon, H. M. and Lockley, R. M. (1933).** "The Grassholm gannets." British Birds, 27, 142–52.

# AN ECOLOGICAL STUDY OF THE INVERTEBRATE FAUNA OF A CHALK STREAM NEAR GREAT DRIFFIELD, YORKSHIRE

By H. WHITEHEAD.

(*With Plate* 3 *and* 4 *Figures in the Text.*)

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## 1. Introduction.

Quantitative methods applied to studying the fauna of the beds of some West Yorkshire streams and rivers have been set forth in the *Journal of Ecology* (**12**, **13**). The sampling there described was done chiefly in the rivers Wharfe and Aire and their tributaries, in regions where the stream beds consisted largely of rock and immovable stones derived from Millstone Grit and Carboniferous Limestone.

A preliminary examination of streams in East Yorkshire, in the chalk area near Driffield, showed that there were marked differences between the physical characters of the stream bed and those of the West Yorkshire stream beds. It seemed desirable that a more detailed examination of a stream bed in the Driffield district should be made and that the fauna should be studied for a period of at least twelve months. Samples were therefore taken from a stream bed, the majority from a measured area of 4 sq. dcm. The Invertebrata—excluding Protozoa and Rotifera—in each sample, were identified as far as possible, and counted. By comparison of these samples it has been possible to form ideas of existing animal communities, to determine what organisms are characteristic in each community, and to investigate seasonal and other changes, including those brought about by floods.

### 2. TOPOGRAPHY AND GENERAL CHARACTERISTICS OF THE STREAM.

The Driffield Trout Stream is in the neighbourhood of Great Driffield in the East Riding of Yorkshire. The water is derived from a number of springs, known locally as "kelds", or "kells", which flow from the chalk formation. Two main branches unite below Driffield to form the River Hull. The northern branch (Elmswell Beck), arising from springs near Elmswell, flows in a south-easterly direction and becomes Driffield Beck before joining the southern branch. The main part of the southern branch arises from springs near Kirk-burn Church, and is known as Eastburn Beck; but, lower in its course, it is marked on the Ordnance six-inch map as Driffield Trout Stream. Two other affluents of the southern branch, shown on the Ordnance map, namely South-burn Beck and Wellsprings Drain, are often dry during summer, and consequently are of little importance to this investigation.

In the shallower parts of the stream, the bed consists of flint flakes and pieces of chalk with a varying amount of silt derived from surface deposits. Aquatic vegetation grows in patches of varying size on the stream bed. There is very little change in the water level of this stream: during drought, the accumulation of vegetation in the river bed has the effect of holding up the water: during periods of flood, the water is let off through sluices (one at Poundsworth Mills and the other at Bell Mills). The stream level was low in September, October, and November of 1929; but when the stream was visited on December 27th, there had been heavy floods which raised the water level about half a metre. The stones at the bottom had been moved along by the current, and the only portions of the stream bed which were stable were in deep water, or in places where aquatic plants (particularly *Sium*) held the drifting stones. There is evidence that normal autumn floods are sufficient to move the flint flakes. The instability of the stream bed has a very important influence on the character of the fauna.

The rate of flow over stony bottom, measured by the Pitôt Tube Method (**11**), was 1·5 metres per second at the surface on June 1st, 1930. The water as a rule is very clear, and has the bluish tinge which is often seen in streams in chalky regions. A sample taken near Bell Mills in May 1928 showed a temporary hardness of 13·5° and a permanent hardness of 4·3° on Clark's Scale. The water was alkaline to litmus paper. The *p*H of the water was determined during the period of investigation by means of a capillator. It varied from 7·6 in January and March to 8·4 in the late summer. This is within the daily range of the *p*H in the River Lark found by Butcher, Pentelow, and Woodley (**2**).

The temperature of the water varied from 7° C. in October and November 1929 to 15° C. in July 1930. No attempts have been made to estimate the oxygen content of the water. The stream flows freely, is clear, free from pollution, and has abundant vegetation: in consequence it was assumed that the oxygen content is not a limiting factor.

The stream is noted for its fine trout, and is controlled by the Driffield Angling Club.

The regions of the stream bed may be classified into:

A. *Beds of stones, sand, silt and mud, without aquatic phanerogams.*

(*a*) *Stony regions* with flakes of flint and chalk fragments of 5 cm. diameter or less. The interstices of the stones are often filled with sand and silt. The current is usually swift, and the water is not often deeper than half a metre.

(*b*) *Silt and mud regions.* These occur in the deeper, slower parts of the stream, e.g. above weirs and sometimes on the lee side of patches of vegetation.

B. *Beds with aquatic phanerogams.*

*Sium erectum* Huds., *Potamogeton perfoliatus* L. and *Ranunculus* spp. are found usually on the more stony parts of the bed, whilst *Hippuris vulgaris* L., *Callitriche* spp. and *Elodea Canadensis* Rich., grow in the deeper water and regions of sand and mud.

Mosses are found only in the Mill races which have not been investigated.

## 3. Methods.

Two methods have been used in this investigation, one for those parts of the stream bed where there were no phanerogamic plants, and the other in regions where these plants abounded.

A. The regions of stone, silt, and mud without phanerogams were sampled by means of the shovel-net. This was first described by Percival and Whitehead (**11**). It consists of a shovel measuring 2 dcm. across the mouth, made of galvanised iron, and provided with a handle. A bag of cellular-woven cotton material is attached to the hind part of the shovel. A flange of leather at the mouth of the bag prevents the escape of small particles. The shovel is thrust into the deposit to a depth of about 5 cm., it having been found that living organisms rarely occur at greater depths than 5 cm. below the level of the stream bed. It is then pushed horizontally forward through a distance of 2 dcm., measured by laying a gauge alongside the shovel on the bed of the stream. By this method a sample of the stream bed of approximately 4 sq. dcm. is taken with the organisms contained therein. The contents of the shovel and net are transferred to a suitable container, and treated with formalin. Subsequent operations are detailed later.

B. The apparatus used for sampling aquatic vegetation was designed by me, and made specially for this investigation (see Pl. 3, Phot. 1). It is a modification of the moss sampler described by Percival and Whitehead (**11**). The sampler for phanerogams consists of a cubical box of galvanised iron of 2 dcm. side. One end is covered by a sheet of brass gauze having square mesh with openings of 0·5 mm. side. The opposite end is open, but can be closed by a sliding lid of galvanised iron, flanged on three sides, while the fourth side has

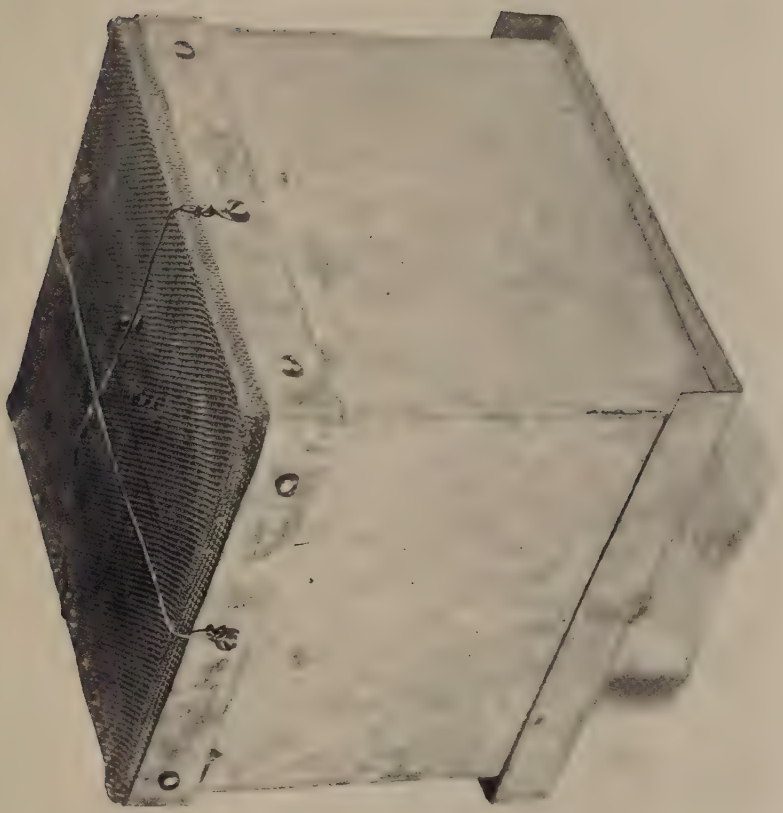

*Photo. H. Whitehead*

Phot. 1. Sampler for aquatic vegetation. Sides of box are two decimetres in length: area of stream bed covered is therefore four square decimetres.

a flat, sharpened edge. The sampler, with the open end downwards, is lowered gently over the water plants until it reaches the floor of the stream. By this means 4 sq. dcm. of the stream bed is covered, the box enclosing the water plants and their contents. The lid is then pushed along the stream bed touching the sampler edges, any resisting plants being cut with a sharp knife. When the lid is in position, the knife is run round the lower edges of the apparatus, which is then lifted out of the water, and turned over in order that the water may run through the sieve, the plants and organisms larger than 0·5 mm. diameter being retained.

The contents of the sampler, including the plants, are emptied into a container and treated with formalin. This apparatus captures nearly all the animals living in the plants from top to bottom over the area. On several occasions, sticklebacks, miller's thumbs, and small lampreys have been caught. The number of animals captured depends largely upon the height of the plants; but as it is intended to compare the numbers of animals living over a unit area of 4 sq. dcm. of stream bed in various parts of the stream, the method appears satisfactory.

On returning to the laboratory each sample is washed separately through a set of three sieves having meshes of 3, 1, and 0·5 mm. respectively. Animals are then picked out, identified and counted. It is not claimed that these methods give precise numerical results. It is claimed, however, that the method enables the *relative* numbers of the commoner animals to be determined. The numerical values are, however, of little importance in dealing with the rarer animals. Another advantage of the method is that all animals in a community are taken into account and dominant species are easily recognised. When using non-numerical methods one is prone to overlook the fact that the most conspicuous animal is not necessarily the commonest.

It was felt that comparisons of the total numbers of the population of one unit of habitat with one unit of another, though giving a clear idea about the number of individual organisms, failed to give any indication of the amount of living animal protoplasm, owing to the differences in size of the organisms. Several attempts were made to express this amount as total weight of organisms taken. These proved unsatisfactory, owing to the difficulties of drying the organisms. A method was finally adopted which consisted of estimating the total volume of the organisms taken in a sample by measuring the volume of water that they displaced. A narrow cylindrical measuring tube of 10 c.c. capacity and graduated into tenths of 1 c.c. was partly filled with water, and a reading taken. The organisms, after surplus moisture had been removed, by placing them for a few minutes on filter-paper, were dropped into the tube, and a second reading taken. The difference between the readings gave the approximate volume of the organisms. The cases of caddis larvae and pupae were removed and the shells of Mollusca were dissolved by dilute hydrochloric acid, before measuring.

A modification and improvement of this simple volumetric method may be of practical value in estimating the amount of fish food available in various parts of a stream, and in expressing the relative biogenic capacity of streams. This method would be of special value in pollutional studies where it might be desirable to compare samples from the same place at intervals of time.

Sampling by quantitative methods was carried on for over a year, the total number of samples being 105, of which 64 were quantitative. From September 1929 to March 1930 samples were taken monthly. No samples were taken during April and May 1930. Fortnightly samples were taken from June to October 1930.

### 4. Stations.

The apparatus used has limited sampling to those regions of the stream in which wading is possible and the bottom can be reached by the hands. A part of the stream between Sunderlandwick Bridge and the Hunting Bridge (station E) proved to be most convenient, as a good variety of bed appears there and wading is easy. Samples were taken from stones and silt. *Sium erectum* and *Ranunculus* sp. At one station (F) the three types occur together within an area of 80 sq. metres, and are described in detail later. A bed of *Hippuris* below Poundsworth Mill and opposite the inset of Driffield Beck (station M) yielded the samples analysed in Table 4.

The upper reaches of Elmswell Beck differ chiefly from the rest of the stream in the fact that when visited a carpet of *Vaucheria* spread over parts of the stream bed. The stony region at Kirkburn was noteworthy for the abundance of *Gammarus* to the almost complete exclusion of other species.

### 5. Animal communities.

(1) *Stony bed.* Tables 1 and 5 give analyses of samples from 4 sq. dcm. of stream bed. The bed, as stated above, consists chiefly of flint flakes and fragments of chalk, with sand and silt in the interstices. This region is unstable during the winter months. The composition of the fauna varies during the year. *Agapetus* (usually *A. fuscipes*) is common during late summer and autumn. *Gammarus* and various species of Oligochaeta (chiefly Tubificidae) are common throughout the year. These may all be regarded as organisms typical of the stony region. Chironomids and *Simulium*, which are common elsewhere, are uncommon in this region. The absence of the latter, which in many districts is a characteristic lithophile, is discussed later. The stony regions are the least prolific in animal life.

(2) *Silt and mud.* This type of stream bed is found chiefly in the still and comparatively deep waters above mill weirs. Analyses of these samples are given in Table 2. One sample taken in March contained *Valvata piscinalis* in large quantities. Species of *Pisidium*, Chironomids and Oligochaetes are characteristic organisms of this region. The difficulties of taking samples with the

Table 1. *Analyses of quantitative samples from stony region.*

| Station ... ... ... ... | E | E | E | E | E | F | F | E | F | F | F | F | F | F | F | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1929 | | | | 1930 | | | | | | | | | | | |
| Date ... ... ... ... | 29. 9 | 27. 10 | 24. 11 | 27. 12* | 26. 1 | 22. 2 | 30. 3 | 15. 6 | 13. 7 | 27. 7 | 10. 8 | 31. 8 | 14. 9 | 28. 9 | 12. 10 | 26. 10 |
| Ancylus fluviatilis | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Physa fontinalis | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . |
| Valvata piscinalis | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Paludestrina jenkinsi | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Chironomidae: (l.) | 2 | 4 | . | 3 | 2 | 2 | 19 | 5 | 15 | 5 | 4 | . | . | 1 | 1 | |
| (p.) | 1 | . | . | . | . | . | . | 2 | 3 | . | . | . | . | . | . | . |
| Ceratopogon sp. (l.) | . | 1 | . | . | . | . | . | . | . | 1 | 5 | . | 2 | . | . | . |
| Dicranota sp. (l.) | . | . | . | . | . | . | . | 8 | 4 | . | 5 | 4 | 2 | . | . | . |
| Ptychoptera sp. (l.) | . | . | . | 12 | . | . | . | . | . | . | . | . | . | . | . | . |
| Simulium spp. (l.) | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | 1 | 1 |
| (p.) | . | . | . | . | . | . | . | . | . | 1 | . | 1 | . | . | . | . |
| Diptera (g. et sp.) | . | . | . | . | 3 | . | . | . | . | . | . | . | . | . | . | . |
| Helmis aeneus: (l.) | . | . | . | 1 | 7 | . | . | . | 5 | 1 | . | 1 | 4 | 3 | . | . |
| (im.) | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Platambus maculatus (l.) | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . |
| Coleoptera (g. et sp.) (l.) | 6 | 11 | 6 | 4 | . | . | . | . | . | . | . | . | . | . | . | . |
| (im.) | 2 | 3 | . | . | . | . | 1 | . | 1 | 1 | 1 | . | 4 | 2 | . | 5 |
| Rhyacophila dorsalis (l.) | . | . | . | . | . | . | . | . | 4 | 1 | . | 1 | 1 | . | . | . |
| (p.) | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | 1 | . |
| Agapetus spp. (l.) | 13 | 125 | 429 | . | 1 | 4 | 5 | 1 | . | 4 | 80 | 34 | 50 | 210 | 230 | 90 |
| (p.) | . | . | . | . | . | . | . | 4 | 14 | . | . | 1 | 3 | 50 | 3 | 30 |
| Polycentropus flavomaculatus (l.) | . | . | . | 3 | . | . | . | . | . | . | . | . | . | . | . | 1 |
| Limnophilidae (l.) | 12 | 2 | 4 | 3 | 3 | . | 1 | 12 | 12 | 3 | 2 | 3 | 8 | 8 | . | 1 |
| (p.) | 12 | 5 | . | . | . | . | . | . | . | . | . | . | . | 4 | . | . |
| Silo pallipes (l.) | . | 5 | 4 | . | . | . | 1 | . | 2 | . | . | 1 | . | 5 | 8 | . |
| (p.) | . | . | 1 | . | . | . | . | . | 2 | . | . | . | . | . | . | . |
| Sericostoma personatum (l.) | . | 1 | 1 | 3 | . | . | . | . | . | . | . | . | . | . | . | . |
| Sialis flavilatera (l.) | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Baetis spp. | . | . | . | . | . | . | . | 14 | 16 | 16 | 25 | 2 | 9 | . | 7 | . |
| Ephemerella ignita | . | . | . | . | . | . | . | 7 | . | 1 | . | . | . | . | . | . |
| Hydracarina | 4 | 5 | 1 | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Gammarus pulex | 91 | 140 | 170 | 21 | 34 | . | 3 | 37 | 111 | 81 | 214 | 65 | 143 | 102 | 50 | 16 |
| Asellus aquaticus | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Ostracods | . | 10 | . | 2 | 1 | . | . | 2 | . | . | . | . | . | . | . | . |
| Piscicola geometra | 1 | . | . | 3 | . | 1 | . | . | . | 1 | 1 | . | 1 | 1 | . | 1 |
| Glossosiphonia complanata | . | . | . | 2 | . | . | . | . | . | . | 1 | 1 | . | . | . | . |
| Helobdella stagnalis | . | . | . | 1 | . | . | . | . | . | . | . | . | 1 | . | . | . |
| Herpobdella sp. | . | 1 | 1 | 2 | 2 | 2 | . | . | 1 | . | . | 1 | 2 | 3 | 1 | . |
| Oligochaetes | 59 | 135 | 78 | 68 | 9 | 4 | 20 | 9 | 85 | 71 | 79 | 96 | 61 | 71 | 37 | 27 |
| Gordius sp. | . | . | . | . | . | . | . | 4 | 2 | . | . | . | . | . | . | . |
| Dendrocoelum lacteum | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Planaria sp. | . | . | . | 6 | 4 | 1 | . | 1 | 2 | . | 5 | . | 4 | 4 | 1 | 1 |
| Total number | 203 | 448 | 695 | 140 | 69 | 15 | 50 | 106 | 279 | 189 | 425 | 212 | 295 | 464 | 340 | 173 |
| Volume in c.c. of: | | | | | | | | | | | | | | | | |
| Insecta | 0·9 | 0·3 | 0·3 | 0·6 | 0·2 | 0·1 | 0·1 | 0·7 | 1·1 | 0·3 | 0·2 | 0·2 | 0·7 | 1·1 | 0·1 | 0·2 |
| Non-insecta | 0·5 | 1·0 | 1·0 | 0·8 | 0·4 | 0·1 | 0·1 | 0·3 | 0·5 | 0·9 | 1·3 | 0·8 | 1·0 | 0·9 | 0·5 | 0·3 |
| Total | 1·4 | 1·3 | 1·3 | 1·4 | 0·6 | 0·2 | 0·2 | 1·0 | 1·6 | 1·2 | 1·5 | 1·0 | 1·7 | 2·0 | 0·6 | 0·5 |

* Floods.

shovel-net in water deeper than half a metre have prevented a series of samples being taken.

Table 2. *Analyses of quantitative samples* (4 *sq. dcm.*) *from mud, from* Callitriche *and from* Potamogeton perfoliatus L.

| | Mud | | *Callitriche* | | *Potamogeton* |
|---|---|---|---|---|---|
| Station ... ... ... ... | M | M | F | G | D |
| Date ... ... ... ... | 26. 3. 27 | 10. 7. 27 | 24. 11. 29 | 22. 2. 30 | 27. 7. 30 |
| Ancylus fluviatilis | . | . | 2 | . | . |
| Limnaea peregra | . | 1 | . | . | . |
| Physa fontinalis | . | . | 25 | 1 | . |
| Valvata piscinalis | 95 | . | . | . | . |
| Pisidium spp. | 35 | 29 | 1 | 15 | . |
| Chironomidae: (l.) | 64 | 14 | 95 | 28 | 53 |
| (p.) | . | . | . | . | 1 |
| Ceratopogon (l.) | 1 | . | . | 3 | . |
| Dicranota sp. (l.) | . | . | . | . | 7 |
| Tipula sp. (l.) | . | . | . | . | 1 |
| Simulium sp. (l.) | 2 | . | 1 | . | 1 |
| Helmis aeneus (l.) | . | . | 17 | . | . |
| Platambus maculatus (l.) | . | . | 4 | . | 2 |
| Hydroptila sp. (l.) | 10 | . | . | . | . |
| Polycentropus flavomaculatus (l.) | 1 | . | 4 | . | . |
| Limnophilidae: (l.) | 3 | . | 70 | 8 | 4 |
| (p.) | . | 5 | 1 | . | . |
| Sericostoma personatum (l.) | 3 | 6 | 1 | . | . |
| Sialis flavilatera (l.) | 1 | 5 | 4 | 16 | . |
| Baetis spp. | 1 | . | . | . | 4 |
| Ephemerella ignita | 2 | . | . | . | 5 |
| Gammarus pulex | 9 | . | 46 | 17 | 41 |
| Asellus aquaticus | . | . | 7 | . | . |
| Piscicola geometra | . | . | 16 | . | 1 |
| Glossosiphonia complanata | . | 2 | . | . | 4 |
| Herpobdella spp. | 1 | . | 7 | . | 3 |
| Oligochaeta | 21 | 49 | 1 | 65 | 62 |
| Dendrocoelum lacteum | . | . | 2 | . | . |
| Planaria spp. | . | . | 9 | . | . |
| Polycelis sp. | . | . | 5 | . | . |
| Total | 249 | 111 | 318 | 153 | 189 |

(3) *Sium erectum* Huds. This is the commonest aquatic phanerogam in the region of the stream under consideration. During spring and summer the radical leaves with their long petioles and flat leaflets furnish abundant shelter for a variety of animals. From December 1929 to February 1930 the current was very strong, owing to heavy rainfall. The older and lower leaves were torn off and washed away. The roots held firm and the projecting stems with smaller leaves held the stones which were being rolled along the stream bed. This resulted in the formation of banks of stones and sand which, on the lee side, gave shelter to some of the smaller animals.

Attempts at sampling the animal life by plucking the plant and filling a 1 lb. jam bottle with it were unsatisfactory, as many of the animals escaped and the quantity of plant taken was not always the same. The method described, which enabled one to take aquatic plants with their animal communities over an area of 4 sq. dcm., was first used on *Sium* in November 1929, and since then twelve similar samples have been taken. Attempts were made in January

Table 3. *Analyses of quantitative samples from* Sium erectum *Huds.*

| | 1929 | | 1930 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date ... ... ... ... | 24. 11 | 27. 12 | 30. 3 | 1. 6 | 15. 6 | 13. 7 | 27. 7 | 10. 8 | 31. 8 | 14. 9 | 28. 9 | 12. 10 | 26. 10 |
| Ancylus fluviatilis | 5 | 3 | . | 10 | . | . | . | . | . | . | 2 | . | . |
| Limnaea peregra | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Paludestrina jenkinsi | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Physa fontinalis | 21 | 1 | 5 | 2 | . | . | . | . | . | . | . | . | . |
| Pisidium sp. | . | . | 3 | 3 | . | 2 | . | . | . | . | . | . | . |
| Chironomidae: (l.) | 30 | . | 6 | 6 | 76 | 44 | 26 | 5 | 6 | 11 | 7 | 3 | . |
| (p.) | . | . | . | . | 11 | 3 | 27 | 35 | . | 1 | 3 | . | . |
| Ceratopogon (l.) | . | . | . | . | . | 2 | . | 1 | . | . | . | . | . |
| Dicranota (l.) | . | . | . | . | 3 | 2 | . | . | . | . | 1 | . | . |
| Tabanid (l.) | . | . | . | 4 | . | . | . | . | . | . | . | . | . |
| Tipulid (l.) | . | . | . | 1 | . | . | . | . | . | . | . | . | . |
| Simulium spp.: (l.) | . | . | 13 | 2 | 134 | 16 | 9 | 57 | 185 | 102 | 345 | 44 | 5 |
| (p.) | . | . | . | . | . | 16 | 18 | 9 | 3 | 13 | 27 | 100 | 8 |
| Diptera g. et sp. | . | 1 | . | 1 | . | . | . | . | . | . | . | . | . |
| Helmis aeneus: (l.) | 16 | 7 | . | . | 7 | . | 1 | 2 | . | . | 2 | . | . |
| Platambus maculatus (l.) | 2 | . | . | . | . | . | . | . | . | . | . | . | 2 |
| Coleoptera g. et sp.: (im.) | . | 1 | . | . | . | 1 | . | . | . | . | 1 | 1 | . |
| Rhyacophila dorsalis (l.) | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Agapetus spp. (l.) | 3 | . | 3 | 1 | 1 | . | . | 1 | . | . | 2 | 3 | 6 |
| Polycentropus flavomaculatus (l.) | 1 | . | . | 3 | . | . | . | . | . | . | 2 | . | 1 |
| Hydropsyche sp. (l.) | . | . | 1 | . | . | . | . | . | . | . | . | . | . |
| Limnophilidae: (l.) | 2 | 6 | 5 | 7 | 12 | . | . | 2 | . | 1 | 6 | 1 | 11 |
| Sericostoma personatum: (l.) | 1 | . | 2 | 2 | 2 | . | . | 1 | . | . | . | . | . |
| (p.) | . | . | . | . | 2 | . | . | . | . | . | . | . | . |
| Sialis flavilatera (l.) | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Baetis spp. | . | . | 6 | 8 | 62 | 60 | 22 | 13 | 15 | 15 | 31 | 28 | 21 |
| Ephemerella ignita | . | . | . | 1 | 4 | 9 | 4 | 8 | 2 | 1 | . | . | . |
| Gammarus pulex | 80 | 47 | 25 | 44 | 38 | 42 | 24 | 70 | 21 | 68 | 126 | 93 | 216 |
| Asellus aquaticus | 20 | 3 | . | . | . | . | . | . | . | . | . | . | . |
| Piscicola geometra | 3 | 2 | . | . | 1 | . | . | 1 | . | . | 1 | 2 | 2 |
| Glossosiphonia complanata | 2 | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Helobdella stagnalis | . | 1 | . | 1 | . | . | . | . | . | . | . | . | . |
| Herpobdella sp. | 3 | . | 2 | 2 | . | 1 | . | . | . | . | . | 2 | 2 |
| Oligochaeta | 12 | 60 | 4 | 20 | 46 | 118 | 6 | 40 | 1 | . | 13 | . | 61 |
| Dendrocoelum lacteum | . | 1 | 3 | . | . | . | . | . | . | . | . | . | . |
| Planaria sp. | 13 | 7 | . | . | 3 | 4 | . | 4 | . | . | 8 | 6 | 8 |
| Total number | 216 | 141 | 78 | 118 | 402 | 320 | 137 | 252 | 234 | 213 | 577 | 283 | 343 |
| Volume in c.c. of: | | | | | | | | | | | | | |
| Insecta | 0·2 | 0·8 | 0·3 | 0·6 | 1·7 | 0·7 | 0·2 | 0·6 | 0·5 | 0·4 | 1·6 | 0·9 | 0·3 |
| Non-Insecta | 3·3 | 2·4 | 0·9 | 1·1 | 0·5 | 0·9 | 0·3 | 0·9 | 0·3 | 1·1 | 1·8 | 1·8 | 2·4 |
| Total volume | 3·5 | 3·2 | 1·2 | 1·7 | 2·2 | 1·6 | 0·5 | 1·5 | 0·8 | 1·5 | 3·4 | 2·7 | 2·7 |

and February to obtain samples but had to be abandoned owing to the floods. Analyses are given in Tables 3 and 5. The total number of animals from *Sium* was least in March, but a rise took place which culminated in mid-June. Then came a steady fall until the end of July. The largest number of individuals taken in this habitat was at the end of September 1930. In mid-June there was a great variety of species; larvae of Chironomids and of *Simulium* were the most abundant, *Baetis* and *Gammarus* coming next. The September rise was due almost entirely to *Simulium*. The dominant organisms on *Sium* are *Simulium*, Chironomids, *Baetis*, *Gammarus*, and Oligochaetes. Limnophilids, though not numerous, are characteristic.

(4) *Ranunculus* spp. This plant occurs in patches in the stony region of the stream and is often associated with *Sium*. Its long, filamentous leaves give shelter to the smaller organisms, and as it never dies down completely, in the winter it forms a valuable plant for the sheltering of animal life. Analyses are given in Table 5. In comparison with *Sium*, *Ranunculus* has a larger animal

population, the numbers being particularly high in July, August, and September.

(5) *Elodea Canadensis*. This plant is not common in the stream. Five samples, not over a measured area, were taken in the months of May, June, July, September and October. Numbers are not quoted here. *Baetis*, *Ephemerella*, and Chironomids are common. Larvae of *Polycentropus flavomaculatus*, though not a common species, are frequently found with this plant.

Table 4. *Analyses of quantitative samples* (4 sq. dcm.) *from* Hippuris vulgaris, *L., from Station M, in* 1930.

| Date ... ... ... ... | 1. 6 | 15. 6 | 13. 7 | 10. 8 | 31. 8 | 14. 9 | 28. 9 | 12. 10 | 26. 10 |
|---|---|---|---|---|---|---|---|---|---|
| Ancylus fluviatilis | 2 | . | . | . | . | . | . | . | . |
| Acroloxus lacustris | . | . | 1 | . | . | . | . | . | . |
| Physa fontinalis | . | . | . | 1 | 36 | 51 | 41 | . | 14 |
| Valvata piscinalis | . | . | 1 | . | . | . | . | . | . |
| Paludestrina jenkinsi | . | . | 66 | 262 | 320 | 22 | 24 | . | . |
| Pisidium sp. | . | . | . | . | . | . | 1 | . | . |
| Chironomidae (l.) | 29 | 420 | 109 | 1 | 2 | 1 | 8 | 1 | 2 |
| (p.) | . | 9 | 7 | 11 | . | . | . | 4 | 4 |
| Ceratopogon (l.) | 2 | 12 | . | . | . | . | 6 | . | . |
| Tabanids (l.) | 2 | . | . | . | . | . | . | . | . |
| Simulium (l.) | . | . | 89 | 8 | 9 | 1 | 5 | 34 | 2 |
| (p.) | . | . | 51 | 4 | . | . | . | 12 | . |
| Helmis aeneus (l.) | 5 | 1 | 8 | 2 | . | 1 | . | . | 1 |
| Platambus maculatus | . | . | . | . | . | . | 1 | . | 1 |
| Coleoptera g. et sp. (Ad.) | . | 2 | 3 | . | . | . | . | . | . |
| Agapetus fuscipes (l.) | . | . | 4 | . | . | . | . | . | . |
| (p.) | . | . | 14 | 4 | . | . | . | 1 | . |
| Hydroptila spp. (l.) | 19 | 11 | . | . | . | . | . | . | . |
| Polycentropus flavomaculatus (l.) | 9 | 2 | 1 | . | . | 1 | 1 | . | . |
| Limnophilidae (l.) | 20 | 8 | . | 5 | . | 1 | 2 | 1 | 1 |
| (p.) | . | . | 1 | . | . | . | . | . | . |
| Sericostoma personatum (l.) | 4 | 2 | . | 1 | . | 2 | . | . | . |
| (p.) | . | . | 1 | . | . | . | . | . | . |
| Sialis flavilatera (l.) | 1 | . | . | . | . | 3 | . | . | . |
| Baetis spp. | 238 | 48 | 200 | 36 | 60 | 37 | 31 | 30 | 9 |
| Ephemerella ignita | 45 | 15 | 150 | 43 | 1 | 3 | . | . | . |
| Gammarus pulex | 21 | 36 | 22 | 45 | 29 | 70 | 47 | 81 | 168 |
| Asellus aquaticus | 13 | . | . | 3 | 2 | 1 | 3 | . | 14 |
| Piscicola geometra | 1 | 2 | . | 6 | 2 | 2 | 1 | 11 | 3 |
| Glossosiphonia complanata | 1 | 1 | 1 | 2 | 3 | 8 | 1 | . | . |
| Helobdella stagnalis | . | . | . | . | . | . | 5 | . | 2 |
| Herpobdella spp. | 16 | 1 | 1 | . | 1 | 4 | 3 | . | 8 |
| Oligochaeta | 28 | 12 | 6 | 12 | 34 | 20 | 28 | . | 122 |
| Planaria spp. | 27 | . | 3 | 4 | 2 | 9 | 8 | 2 | 9 |
| Polycelis spp. | 21 | . | . | . | . | . | . | . | . |
| Total number | 504 | 582 | 739 | 450 | 501 | 237 | 216 | 177 | 360 |
| Volume in c.c. of: | | | | | | | | | |
| Insecta | 2·6 | 1·8 | 3·5 | 0·9 | 0·3 | 0·3 | 0·1 | 0·3 | 0·2 |
| Non-Insecta | 0·9 | 0·3 | 0·4 | 1·9 | 2·0 | 2·2 | 1·6 | 2·1 | 5·3 |
| Total volume | 3·5 | 2·1 | 3·9 | 2·8 | 2·3 | 2·5 | 1·7 | 2·4 | 5·5 |

(6) *Hippuris vulgaris* L. This plant grows in the deeper water, and the length of stem is usually proportional to the depth of the water. All the samples taken were from water about half a metre deep: they were fourteen in number. A conveniently situated patch of this plant was found at the junction of Driffield Beck with Driffield Trout Stream. Nine quantitative samples, each

of 4 sq. dcm., were taken from an area of about 2 sq. metres at intervals from June to October. The analyses are given in Table 4. The plant appears to be eminently suitable for the shelter of most kinds of aquatic invertebrates, and the total number of organisms per 4 sq. dcm. varied from 177 to 739. Chironomid larvae were very abundant in June, but the numbers fell off rapidly later in the year. Hippuris is a favourite habitat for *Baetis*, and *Ephemerella*, and it was noted on several occasions that subimagines of these genera were hatching out in numbers over submerged patches of the plant.

(7) *Callitriche* spp. Patches of *Callitriche* were sampled on eight occasions, but of these, three only were quantitative. Analyses are given in Table 2. One sample taken in December 1929, in a ditch with flowing water, had over 500 specimens of *Paludestrina* and comparatively large numbers of Limnophilids. The larvae of one species, *Anabolia nervosa*, are common in this plant. *Baetis* and *Ephemerella* are not abundant, and Chironomids have never reached high numbers in the samples taken.

### 6. Animal communities compared.

It might be urged that it would be of little value to compare the species and numbers of animals found in one sample with those taken in another

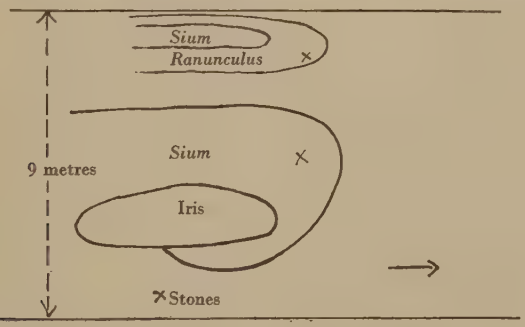


Fig. 1. Sketch-map of stream at station F. The crosses show the places at which samples were taken.

sample from a different part of the stream, since a large number of factors are involved, such as depth of water, rate of current, light and shade, as well as local differences due to the incoming of small tributaries. Again, the presence of cattle in certain regions tends to stir up the fine material of the bed. One portion of the stream, however, above Sunderlandwick Bridge, offered a marked variety of habitats in a small area, as shown in the sketch-map above (Fig. 1).

A line 8 metres in length drawn aslant across the stream would pass through a stony bed, a patch of *Sium*, and one of *Ranunculus*. Eight samples have been taken from each of these three regions at intervals extending from July to

Table 5. *Comparison of the faunas of three types of stream bottom.* *Stones*, Ranunculus *and* Sium, *in close proximity at Station F.*

| Date | 13. 7. 30 | | | 27. 7. 30 | | | 10. 8. 30 | | | 31. 8. 30 | | | 14. 9. 30 | | | 28. 9. 30 | | | 12. 10. 30 | | | 26. 10. 30 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stream bed | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* | Stones | *Ran.* | *Sium* |
| Physa fontinalis | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2 | . | . | . | . | . | . |
| Valvata piscinalis | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Paludestrina jenkinsi | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | 1 | . | . | . | . | 3 | . | . | . | . |
| Pisidium spp. | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Chironomidae: (l.) | 15 | 456 | 44 | 5 | 138 | 27 | 4 | 520 | 38 | . | 294 | 6 | . | 150 | 11 | 1 | 88 | 7 | 1 | 117 | 3 | . | 34 | . |
| (p.) | 3 | 13 | 3 | . | 6 | 26 | . | 16 | 2 | . | 5 | . | . | 7 | 1 | . | 10 | 3 | . | 7 | . | . | 3 | . |
| Ceratopogon spp. (l.) | . | . | 2 | 1 | . | . | 5 | . | 1 | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . |
| Dicranota spp. (l.) | 4 | . | 2 | . | . | . | 5 | . | . | 4 | . | . | 2 | . | . | . | . | 1 | . | . | . | . | . | . |
| Simulium: (l.) | . | 112 | 16 | 2 | 20 | 18 | . | 128 | 57 | . | 617 | 185 | . | 17 | 102 | . | 181 | 345 | 1 | 34 | 44 | 1 | 26 | 5 |
| (p.) | . | 9 | 16 | 1 | 5 | 9 | . | . | 9 | 1 | 31 | 3 | . | 3 | 13 | . | 26 | 27 | . | 28 | 100 | . | 9 | 8 |
| Helmis aeneus (l.) | 5 | 13 | . | 1 | 4 | 1 | 1 | 5 | 2 | 1 | 5 | . | 4 | 1 | . | 3 | 1 | 2 | . | 2 | . | 5 | 2 | . |
| Platambus maculatus (l.) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 |
| Beetle (g. et spp.) | 1 | . | 1 | 1 | . | . | 1 | 1 | . | . | 1 | . | 4 | 2 | . | 2 | . | 1 | . | . | 1 | . | 1 | . |
| Rhyacophila dorsalis: (l.) | 4 | 1 | . | 1 | 2 | . | . | 5 | . | 1 | 3 | 1 | 1 | . | . | . | . | . | . | 1 | 3 | . | 2 | . |
| (p.) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Agapetus fuscipes: (l.) | . | . | . | 4 | . | . | 80 | 2 | 1 | 34 | . | . | 50 | . | . | 210 | 8 | 2 | 230 | 4 | . | 90 | 1 | 6 |
| (p.) | 14 | . | . | . | . | . | . | . | . | 1 | . | . | 3 | . | . | 50 | 1 | . | 3 | . | . | 30 | 2 | . |
| Polycentropus flavomaculatus (l.) | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | 4 | 2 | . | 3 | . | 1 | 10 | 1 |
| Limnophilidae (l.) | 12 | . | . | 3 | 2 | . | 2 | . | 2 | 3 | . | . | 8 | 3 | 1 | 8 | 8 | 6 | . | 11 | 1 | 1 | 7 | 11 |
| (p.) | . | 1 | . | . | 1 | . | . | 1 | . | . | . | . | . | . | . | 4 | . | . | . | . | . | . | . | . |
| Silo pallipes (l.) | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| (p.) | 2 | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | 5 | . | . | 8 | . | . | . | . | . |
| Sericostoma personatum: (l.) | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| (p.) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Baetis spp. | 16 | 111 | 60 | 16 | 33 | 22 | 25 | 30 | 13 | 2 | 49 | 15 | 9 | 82 | 15 | . | 94 | 31 | 7 | 70 | 28 | . | 36 | 21 |
| Ephemerella ignita | . | 71 | 9 | 1 | 23 | 4 | . | 8 | 8 | . | 19 | 2 | . | 16 | 1 | . | 5 | . | . | 4 | . | . | . | . |
| Hydracarina | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Gammarus pulex | 111 | 26 | 42 | 81 | 23 | 24 | 214 | 32 | 70 | 65 | 50 | 21 | 143 | 42 | 68 | 102 | 82 | 126 | 50 | 36 | 93 | 16 | 73 | 216 |
| Asellus aquaticus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . |
| Piscicola geometra | . | . | . | 1 | . | . | 1 | 23 | 4 | . | 16 | . | 1 | 14 | . | 1 | 13 | 1 | . | 23 | 2 | 1 | 3 | 2 |
| Glossosiphonia complanata | . | . | . | . | . | . | 1 | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Helobdella stagnalis | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . |
| Herpobdella spp. | 1 | . | 1 | . | . | . | . | . | . | 1 | . | . | 2 | . | . | 3 | . | . | 1 | . | 2 | . | . | 2 |
| Oligochaeta | 85 | 1 | 118 | 71 | 3 | 6 | 79 | 6 | 40 | 96 | 11 | 1 | 61 | 5 | . | 71 | . | 13 | 37 | 2 | . | 27 | 10 | 61 |
| Gordius sp. | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Planaria sp. | 2 | . | 4 | . | . | . | 5 | 3 | 4 | . | . | . | 4 | . | . | 4 | 4 | 8 | 1 | 1 | 6 | 1 | 8 | 8 |
| Polycelis nigra | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 8 | . | . | . | . |
| Total numbers | 279 | 811 | 320 | 189 | 260 | 137 | 125 | 781 | 252 | 212 | 1101 | 234 | 295 | 342 | 213 | 464 | 526 | 577 | 340 | 354 | 283 | 173 | 228 | 343 |
| Volume in c.c. of: | | | | | | | | | | | | | | | | | | | | | | | | |
| Insecta | 1·1 | 2·0 | 0·7 | 0·3 | 0·8 | 0·2 | 0·2 | 1·2 | 0·6 | 0·2 | 2·3 | 0·5 | 0·7 | 0·7 | 0·4 | 1·1 | 1·6 | 1·6 | 0·1 | 1·0 | 0·9 | 0·2 | 0·9 | 0·3 |
| Non-Insecta | 0·5 | 0·6 | 0·9 | 0·9 | 0·3 | 0·3 | 1·3 | 0·5 | 0·9 | 0·8 | 0·5 | 0·3 | 1·0 | 0·5 | 1·1 | 0·9 | 1·2 | 1·8 | 0·5 | 0·7 | 1·8 | 0·3 | 1·4 | 2·4 |
| Total volume | 1·6 | 2·6 | 1·6 | 1·2 | 1·1 | 0·5 | 1·5 | 1·7 | 1·5 | 1·0 | 2·8 | 0·8 | 1·7 | 1·2 | 1·5 | 2·0 | 2·8 | 3·4 | 0·6 | 1·7 | 2·7 | 0·5 | 2·3 | 2·7 |

October 1930. For the sake of comparison, the analyses of these have been brought together in Table 5.

There are notable differences between the fauna of the stones and that of the adjacent vegetation. *Agapetus* was found in considerable numbers in the stony region, but was absent from the plants. On the other hand, Chironomids and *Simulium*, which are abundant in the latter, are seldom found in the former. Stray individuals of *Baetis* and *Ephemerella* may reach the stony region, though their favourite haunt is undoubtedly amongst the plants.

When we compare the fauna living in *Ranunculus* with that living in *Sium*, we find that in the case of *Simulium* and *Gammarus* sometimes one habitat and sometimes the other has the greater number. On every occasion there were more Chironomids in *Ranunculus* than in *Sium*, and the same preference applies to nymphs of *Baetis* and *Ephemerella*. At the present I have no satisfactory explanation of these differences to offer. During the months of July and August the total population in a patch of *Ranunculus* was far in excess of that in *Sium*, but from August to the end of October the numbers were nearly equal. This is traceable to the fact that *Simulium* and Chironomids were leaving the stream in considerable numbers as winged insects.

### 7. Food of the invertebrate fauna.

Observations have been made on the gut contents of some of the invertebrates. These observations confirm the findings of Percival and Whitehead (**12**, p. 311) that few stream Invertebrata feed upon phanerogams, but that there is plenty of evidence that they feed freely on the microflora and microfauna. Lumps of algae (*Gomphonema*) were abundant on *Hippuris* in March 1930, and in June the filamentous algae *Vaucheria* and *Batrachospermum* were abundant. In June, masses of brown flocculent material, consisting chiefly of diatoms, rose from parts of the stream bed. The only observed case of damage done to phanerogams by an invertebrate was that in which *Anabolia nervosa* was cutting off the leaves of *Callitriche* in order to make its larval case.

A considerable amount of animal matter, such as earthworms and insect larvae, which normally live on the banks, finds its way into the stream throughout the year. This furnishes food for carnivores and detrital feeders.

### 8. Seasonal changes.

The number of animals in any habitat in the stream is subject to great variation especially during the warmer periods of the year. This is particularly the case with insects. Many of the stream insects have more than one brood per annum. In most cases the nymphal stages are short. In the case of Chironomids, Goetghebuer (**7**) says: "La vie larvaire peut durer plusieurs semaines ou même des mois, mais la vie nymphale est courte. A la température de 19°, la nymphose dure environ 60 heures (Comas)." The effect of this may be

Table 6. *List of the typical invertebrates from the Driffield trout stream, showing the stages in the life cycle and the months in which they have been found.*

| | Jan. | Feb. | Mar. | April (1928) May 1931 | May 1931 | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis (O.F.M.) | . | . | + | + | + | + | + | . | + | . | - | - |
| Acroloxus lacustris (L.) | . | . | + | . | + | + | + | . | + | + | - | - |
| Limnaea peregra (O.F.M.) | . | - | + | . | + | . | + | . | . | . | - | - |
| Physa fontinalis (L.) | + | + | + | . | + | + | . | + | + | + | - | - |
| Valvata piscinalis (O.F.M.) | . | . | + | . | . | . | + | + | . | . | . | . |
| Paludestrina jenkinsi Smith | - | . | . | . | . | . | + | + | + | + | . | . |
| Pisidium spp. | + | + | + | . | + | + | + | + | + | . | - | + |
| DIPTERA | | | | | | | | | | | | |
| Chironomidae | L | L, P | L, P | L | L, P | L, P | L, P | L, P | L, P | L, P | L | L |
| Ceratopogon spp. | . | L | . | . | . | L | L | L | L | L | . | . |
| Dicranota spp. | . | . | . | . | . | L | L | L | L | . | . | . |
| Simulium spp. | . | . | L | L, P | L, P | L | L, P | L, P | L, P | L, P | L | L |
| COLEOPTERA | | | | | | | | | | | | |
| Brychius elevatus Panz. | . | . | . | . | . | L | L | . | L | . | . | L |
| Platambus maculatus L. | L | . | . | . | . | . | L | . | L | L | L | L |
| Helmis aeneus Müll. | L | L | L, A | L | L, A | L | L, A | L | L, A | L, A | L | L |
| TRICHOPTERA | | | | | | | | | | | | |
| Rhyacophila dorsalis Curt. | L | P | P | . | L, P | . | L, P | L | L | L | . | L, P |
| Agapetus fuscipes Curt. | L | L | L, P | L | L, P | L, P | L, P | L, A, P | L, P | L, P | L | L |
| Polycentropus flavomaculatus Pict. | L | . | L | L | . | L | L | L | L, A | L | . | L |
| *Limnophilidae | L | L | . | L | L | L | L | . | L, P | L, P | L | L |
| Silo pallipes Fbr. | . | . | L, P | L | L, P | . | L, P | L | L | L | L, P | . |
| Sericostoma personatum Spence | . | L | . | . | L | L, P | P | A, L | A, L | L | L | L |
| PLANIPENNIA | | | | | | | | | | | | |
| Sialis flavilatera L. | L | L | L | . | L | L | . | . | L | . | L | L |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis spp. | . | . | N | N | N | N | N | N | N | N | . | . |
| Ephemerella ignita Poda | N | . | N | . | N | N | N | N | N | . | . | . |
| CRUSTACEA | | | | | | | | | | | | |
| Gammarus pulex (L.) | - | E, + | E, + | + | E, + | E, + | E, + | E, + | E, - | E, - | + | E, + |
| Asellus aquaticus | - | + | . | + | . | - | + | + | + | + | - | - |
| HIRUDINEA | | | | | | | | | | | | |
| Piscicola geometra L. | + | + | - | + | + | . | + | + | + | + | + | - |
| Glossosophonia complanata L. | . | - | + | . | + | + | + | + | + | + | + | + |
| Helobdella stagnalis L. | . | . | . | . | . | + | . | . | + | - | . | + |
| Herpobdella spp. | + | | + | + | c. + | c, + | + | + | + | + | + | + |
| OLIGOCHAETA | c, + | + | + | + | c. + | c. + | c, + | + | + | c, + | + | c, + |
| TRICLADIDA | | | | | | | | | | | | |
| Dendrocoelum lacteum (Müll.) | . | . | + | . | . | . | + | . | . | . | + | - |
| Planaria polychroa (?) | + | + | + | + | + | + | + | + | . | + | + | + |
| Polycelis spp. | . | . | + | . | + | + | + | . | + | + | + | . |

A, adult. c, cocoon. E, eggs. L, larva. N, nymph. P, pupa.

* See p. 75.

seen in a series of samples taken from *Ranunculus* at intervals from July to October 1930, when the numbers of Chironomids and of *Simulium* (larvae and pupae) ran as shown below. No doubt several species were concerned in each case.

| Dates ... | 13. 7 | 27. 7 | 10. 8 | 31. 8 | 14. 9 | 28. 9 | 12. 10 | 26. 10 |
|---|---|---|---|---|---|---|---|---|
| Chironomids | 469 | 144 | 536 | 299 | 157 | 98 | 124 | 37 |
| *Simulium* | 121 | 25 | 128 | 648 | 20 | 207 | 62 | 35 |

In Table 4, showing the population in *Hippuris*, there are two dates on which *Baetis* was exceptionally numerous—June 1st and July 13th, 1930. A slight rise took place again at the end of August. At least two species of *Baetis* have been taken on the wing at Driffield—*B. bioculatus*, and *B. tenax*. The explanation of the August rise is complicated by the fact that both species

may be concerned in it. Very little appears to be known about the duration of life in species of *Baetis*. Ulmer (**15**), quoting H. E. Murphy, states that *B. posticatus*, a North American species, has three broods in two years.

In the case of *Ephemerella ignita*, full-sized nymphs are found only occasionally during the winter months. These have most probably been late in developing, and have failed to reach their penultimate instar before the winter weather set in. Temperature, however, is not the only factor involved. This species has frequently been seen on the wing in cold windy weather. The

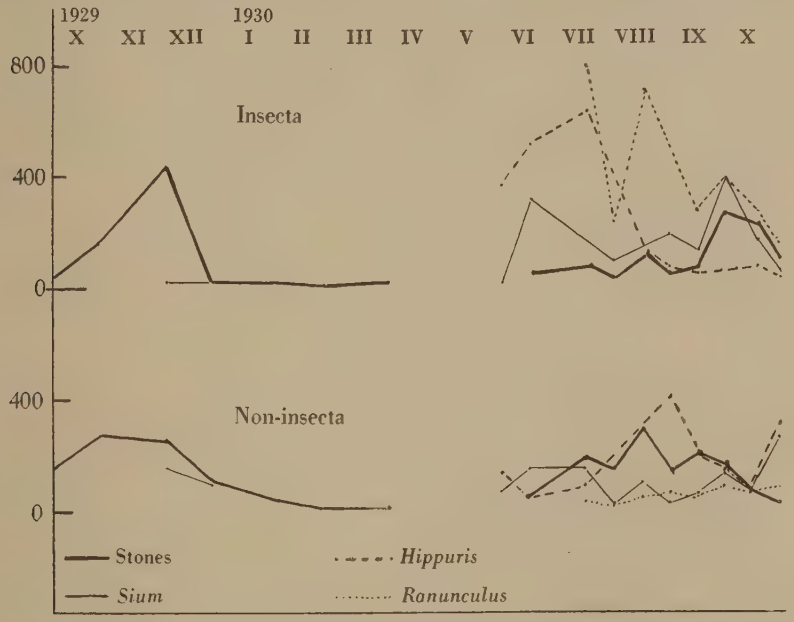


Fig. 2. Diagrams showing the change in numbers of invertebrates on equal areas of four kinds of stream bed: stones, *Sium*, *Ranunculus* and *Hippuris*. The upper diagram refers to the number of insect larvae and nymphs. The lower diagram shows the numbers of invertebrates other than insects.

number of nymphs in *Ranunculus* and *Hippuris* attains its maximum in mid-July, after which there is a gradual falling off. The figures shown in Table 5 fit in well with what is known of the life history of *Ephemerella ignita*. Although imagines may be taken from mid-June to mid-September, it is very probable that there is only one brood per annum. The eggs have a long incubation period. Mosely (**9**) states that eggs take six months to incubate in a London greenhouse.

There appears to be only one brood per annum in the case of *Agapetus* also. This point will be discussed later.

It will be seen from the above that the insect population presents many difficulties, owing to the fact that insects leave the water in great numbers during the summer, and that some have more than one brood in a season. In considering the variations in the population of the stream, it was deemed advisable to separate the transitory insect population from that consisting of permanently aquatic organisms. The diagrams (Fig. 2) indicating the number of insects taken at intervals from four types of habitat, show great variation, especially in late summer and autumn. The lower diagram shows that the non-insect population, though less numerous, is more stable.

Another point of interest bearing on seasonal changes in the general population is indicated in the above diagrams. During October 1930 a steady decrease in the number of insects is shown. Many larvae at this season would be very small, and may have passed through the sieve, or have been overlooked

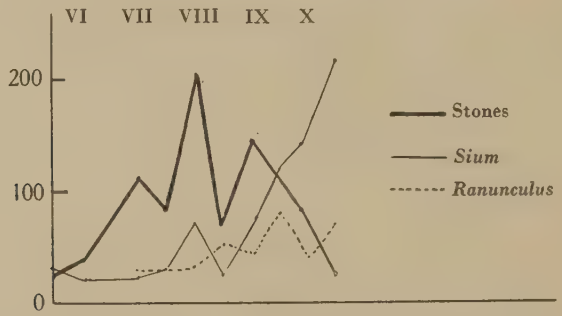


Fig. 3. Diagram showing the numbers of *Gammarus* found over equal and adjacent areas of three types of stream bed: stones, *Sium*, *Ranunculus*, from June to October 1930. Compare the falling off in numbers in the stony region with the rise in regions of aquatic vegetation.

during the examination of samples. This is the case in each habitat given. On the other hand, whilst the non-insect population in the stony regions is still falling, the population in the vegetation is rising. There is distinct evidence here of a shifting of the population from the current-swept stones to the shelter of the plants. It does not follow that migration has been voluntary, and it seems to be more probable that the current has swept the organisms down stream, and they have taken shelter in the comparatively still water between leaves and stems of plants.

The greater part of the non-insect population consists of *Gammarus*. The diagram (Fig. 3) indicates the autumnal changes in the distribution of this crustacean in stony regions, in *Sium*, and in *Ranunculus*.

The increase in numbers in *Sium* coinciding with the fall in numbers in stony regions is very marked. It was noted, too, that the specimens of *Gammarus* taken from the stony region during October were much smaller than those from *Sium*, and the explanation seems to be that while the smaller

*Gammarus* would find shelter in the spaces between the stones, the larger animals would be unable to do so owing to their greater size. Percival and

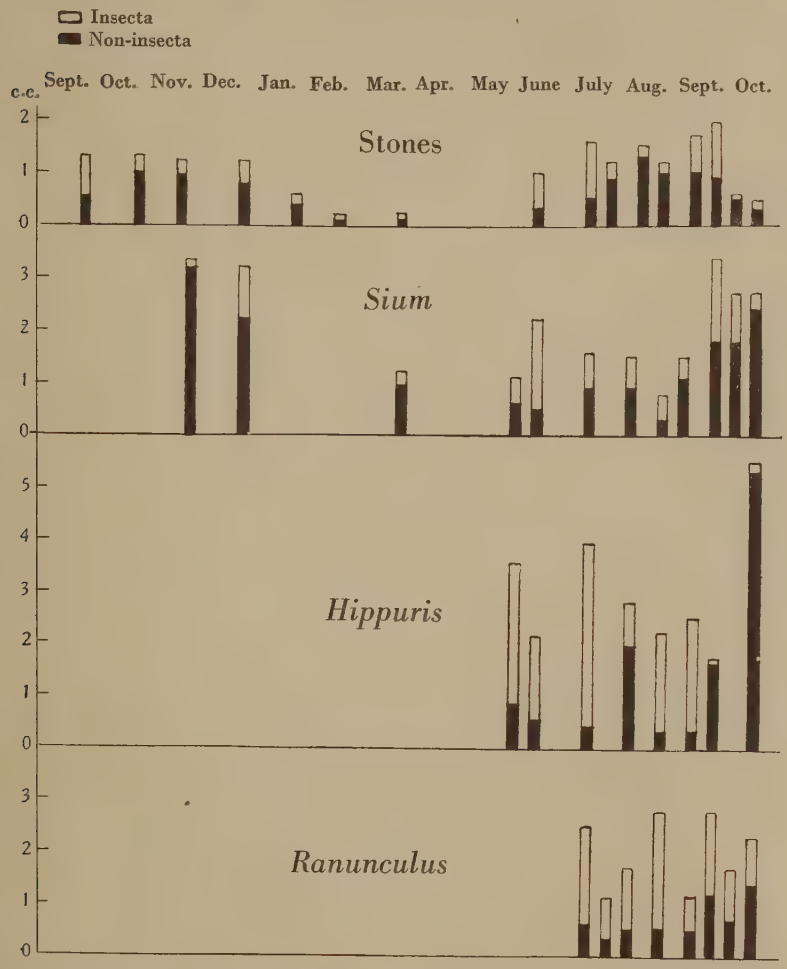


Fig. 4. Diagram showing the changes in volume (expressed in c.c.) on four types of stream bed at different seasons. This contrasts the autumnal fall in non-insecta in the stony region with an autumnal rise amongst the plants *Sium*, *Hippuris* and *Ranunculus*.

Whitehead (**12**) found that *Gammarus* usually took to shelter when the current was strong enough to transport fine sand.

The differences between the changes in population of the stony region during the autumn of 1929 and of 1930 require consideration. In 1929 the

unusually severe summer drought was not broken until December, when floods occurred: in 1930 there had been a good deal of rain throughout the summer. In 1929 a fall in the population of the stony region began in November: in 1930 a similar fall occurred two months earlier, that is, in September.

When we come to the consideration of the volume of animal life measured in c.c., which may be regarded as the quantity of fish food available at various seasons, similar variations are shown. Again, there is a marked falling off in animal life in the stony regions in the late autumn, and a marked rise in the parts of the stream rich in vegetation (see diagram in Fig. 4). The great increase in the volume of Invertebrata in the autumn is noteworthy, though a very small proportion of that increase is due to insects.

The large number of trout living in this stream must have a considerable effect upon the other forms of life. February is the chief spawning month for trout at Driffield. This is much later than on the River Derwent, about twenty miles north, where it takes place in November and December. The Driffield trout feed very little during November and December, at a time when the invertebrate population is falling in both the stony regions and in *Sium*. Unfortunately, it has been impossible to get satisfactory samples of *Hippuris* and *Ranunculus* at this season. There are not sufficient data to determine the amount and influence of trout upon other forms of life.

### 9. Observations on some of the commoner stream Invertebrata.

Table 6 shows stages in the life cycle of typical Invertebrata with the months in which they have been found.

#### *Mollusca.*

On the whole, Mollusca are not common in the parts of the stream sampled. *Physa fontinalis* is found more frequently than *Limnaea peregra*. *Paludestrina jenkinsi* has a rather remarkable distribution in the stream. It was found at the junction with Driffield Beck (below Poundsworth Mills) in great numbers from July to September 1930, but was not taken in June or October. It is comparatively rare in the main stream above Poundsworth Mills, but occurred in great abundance in December 1929 and January 1930 in a drain which comes from Kellythorpe, and joins the main stream below the Mill dam. A possible explanation of this is that *Paludestrina* is extending upstream, but had failed to get through the Mill race. A similar obstacle would be met with at Bell Mills, but in this case there is a route alternative to the Mill race. From reports it appears that large numbers of this mollusc are taken from stomachs of trout caught in the stream.

#### *Diptera.*

The Chironomids occur in large numbers, and although representatives of the groups Tanytarsids and Tanypodinae have been identified, their relative numbers have not been counted. Larvae of biting flies of the genus *Simulium*

are abundantly represented, but no attempt has been made to identify species from larvae. Identification of pupae by a key published by Edwards (**6**) is comparatively easy. The following species have been identified from Driffield: *S. ornatum* was found abundantly from July to October: *S. latipes* and *S. equinum* were frequent during the same period: *S. variegatum* and *S. angustitarsis* are not common. There is no evidence of seasonal periodicity in this genus.

*Trichoptera* (*Caddis-flies*).

*Agapetus fuscipes* is very common in the larval stages in stony regions from spring to late autumn. Its appearance and disappearance during the year are noteworthy. From September to November 1929 the number of small larvae rose steadily to 429 per 4 sq. dcm. On the next visit (December 27th) the stream was in flood, and no larvae of *Agapetus* were found. It seemed probable that the small larvae had been washed into deeper and quieter waters. During the months of January and February careful search was made lower down the stream, but only odd individuals were found. At the end of March, however, *Agapetus* was found in its old haunts, numbering 60 per 4 sq. dcm., the larvae having grown considerably since November. Pupae were found in mid-June and July. At the end of September a sample from 4 sq. dcm. had 50 pupae, 60 large larvae, and 150 small larvae. There was no doubt that the small larvae had been hatched during the summer of 1930 and that the large larvae and pupae belonged to the 1929 brood, that is to say, there is one brood per annum. During October only pupae and small larvae of 1930 were found. There were no large larvae or pupae found during September and October 1929 and there appears to be no doubt that the dull summer of 1930 retarded development, or, alternatively, that the bright summer of 1929 hastened it.

The larvae of Limnophilidae are difficult to identify, and consequently they have not been individually considered in this paper. Imagines have been taken and the species identified with certainty. Determination of genera in the case of pupae presents no great difficulty. The following species occur on the Driffield Trout Stream: *Anabolia nervosa*, *Chaetopteryx villosa*, *Halesus tesselatus*, *Limnophilus lunatus*, *L. extricatus*, and *L. nigriceps*.

*Ephemeroptera* (*May-flies*).

The genera *Baetis* and *Ephemerella* comprise nearly the whole may-fly population, and points of interest concerning them have been discussed on p. 71. Only one nymph of *Ephemera danica* has been found. Its absence from this stream is explained by the fact that there are few places with a sandy bed suitable for the oviposition and the development of the larvae of this species (**11**).

*Plecoptera* (*Stone-flies*).

Representatives of this order are noticeably few in the Driffield area. A few nymphs of *Chloroperla grammatica* and *Nephelopteryx nebulosa* have been taken.

*Crustacea.*

The shrimp, *Gammarus pulex*, is undoubtedly the commonest invertebrate in the streams under consideration. Occurring in all regions, it appears at all times of the year. Females bearing eggs have been found in every month, with the exception of January, April, and November, and no doubt they occur also in these months. According to Chevreux and Fage (**4**) the usual number of eggs carried by this species is 27. Very little work seems to have been done on the life history of this species. Haempel (**8**) found in Bavaria that the species lives chiefly in running water, and that reproduction continues uninterruptedly both in summer and winter. Each female produces, on an average, three broods and then dies or becomes sterile. The brood becomes sexually mature in three months. Dahl (**5**), who studied the species of Norway, found notable differences. There, it is confined to comparatively still waters (lakes), and reproduction takes place only during summer months. *Gammarus pulex* in the Driffield Trout Stream more closely resembles the southern European forms, both in habitat and in seasonal behaviour. Its omnivorous habits no doubt are an important factor in determining its wide distribution in the stream.

*Hirudinea* (*Leeches*).

*Piscicola geometra* is abundant on vegetation where it lies in wait for the fish upon which it preys. It is of interest to note the association of other species of leeches with their prey. *Glossosiphonia complanata* and *Helobdella stagnalis* prey upon Gastropods. Though these leeches may be absent from samples containing Mollusca, they rarely occur in samples which do not contain their prey. The genus *Herpobdella* feeds upon Oligochaetes and Chironomids, and are usually found where such food abounds.

## 10. Comparison of Driffield Trout Stream with the River Wharfe.

The Driffield streams and the upper reaches of the River Wharfe both run through districts in which calcium carbonate is abundant—as chalk at Driffield, and as Carboniferous limestone on the Wharfe. Their faunas, however, differ in many respects, and this is due chiefly to the fact that the stream bed of the Wharfe is more stable than that of Driffield Trout Stream. The larger blocks of limestone in the Wharfe are seldom moved by the current, and in some places they are cemented to the bottom: on the other hand, the bed of the Driffield Trout Stream has small stones which are often moved. Blocks of stone give shelter to many organisms: nymphs of the *Ecdyonurus* and *Rhithrogena*, common in the Wharfe, are absent from Driffield. Another feature of ecological interest is that some genera, such as *Simulium*, found on the immovable stones in the Wharfe, are not found in the stony regions at Driffield, but are attached to the more stable vegetation. The caddis-fly, *Agapetus*, occurs, sometimes in great numbers, on leaves of *Iris* at Driffield. Another

difference is to be noted. The stones in the Wharfe are usually covered with moss, which shelters a specific fauna (**12**). At Driffield, the stones never bear moss: it grows only in the brick-lined Mill races. On the other hand, the Driffield streams have abundant phanerogamic vegetation, and amongst it are found many species which are found amongst moss in the River Wharfe.

These observations show that the nature of the stream bed is a factor of the greatest importance in determining the nature of the fauna. Its influence is both direct and indirect: directly, it determines the nature of the shelter offered to animals and indirectly it influences the nature of the plant growth.

## 11. SUMMARY.

1. The nature of the stream bed influences in a marked degree the nature of the fauna. Not only is the presence or absence of aquatic phanerogams a factor of primary importance, but there is also a notable difference in the constitution of the animal communities living among different species of aquatic plants. This is well shown in the case of *Sium* and *Ranunculus* growing within a few feet of each other.

2. The insect population, as would be expected, is the most variable part. This is particularly the case with species having more than one brood per annum. Species having only one brood, such as *Ephemerella ignita* and *Agapetus fuscipes*, show a steady rise to a maximum and then a gradual fall.

3. The numbers of large insect larvae diminish rapidly in autumn and the majority of insects spend the winter either as very small larvae or as eggs, and so escape notice. On the other hand, the number of non-insect Invertebrata increases rapidly in autumn.

4. There is a definite redistribution in the population of the stream bed with the coming of the autumn floods. The number of animals in the stony regions falls rapidly, whilst there is a corresponding rise amongst the submerged plants. A good example of this change of habitat is shown in the shrimp *Gammarus pulex*. There were marked differences in the dates of this redistribution of the fauna in the autumn of 1929 and of 1930. It was much later in the drier season of 1929 than in the comparatively wet season of 1930.

5. Comparison of the fauna of the Driffield chalk stream with that of a stream in a limestone region (River Wharfe) shows a marked difference due chiefly to the fact that the stony parts of the bed of the River Wharfe are more stable than the stony regions of the chalk stream. The most stable parts of the Driffield stream are those with submerged phanerogams. Some organisms, for example, *Simulium*, are definitely lithophile in the River Wharfe, and phytophile at Driffield.

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# THE FEEDING GROUNDS OF ROOKS AND OTHER BIRDS

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Several workers have recently made use of observations from the train and other moving vehicles, when dealing with the numbers and distribution of birds. The following observations were made from the train, on the type of fields in which the birds were seen and not on their actual numbers. A similar method is mentioned by Elton in his book on *Animal Ecology* (1927, p. 144). He only dealt with pasture and newly-sown corn fields, and found a higher percentage of the latter with rooks, although these fields were less numerous.

The method employed in this investigation was to note every field next to the line as it was passed, using a suitable symbol to show the type of field and the species of birds it contained. Each station was recorded, so that the locality of the observations could be determined from a map. Further, the time was noted, in order to avoid including observations late in the day, as it was found that the movements of the flocks of birds preparatory to roosting greatly affected their distribution. The data were collected during 15 journeys in 1932 and 1933, in the summer and winter months only. The earliest date was July 11th and the latest January 12th. Rooks (*Corvus frugilegus*) were the most plentiful birds seen, as well as the most conspicuous, but the occurrence of starlings (*Sturnus vulgaris*) and lapwings (*V. vanellus*) was also recorded. A few other birds were occasionally seen, but their numbers were too small to be worth consideration. Out of a total of 3834 fields, only 12 had wood pigeons (*Columba palumbus*); 3, pheasants (*Phasianus colchicus*); 2, blackheaded gulls (*Larus ridibundus*); 1, partridges (*P. perdix*).

Table 1. *The dates and localities of the observations.*

| | | | | | |
|---|---|---|---|---|---|
| 1932 | Jan. 12th | Cricklade to Birmingham. | 1933 | Jan. 9th | Crewe to Stockport. |
| | July 11th | Salisbury to Honiton. | | July 19th | Stockport to Rugby. |
| | July 23rd | Plymouth to Bristol. | | July 27th | Croydon to Newhaven. |
| | Aug. 22nd | Southampton to Stockport. | | Aug. 28th | Ludgershall to Swindon and Crewe to Stockport. |
| | Aug. 31st | Leeds to York. | | Sept. 6th. | Chinley to Leicester. |
| | Sept. 7th | York to Leeds. | | Sept. 10th | Leicester to Ambergate. |
| | Oct. 7th | Crew to Rugby. | | | |
| | Oct. 8th | Berkhampstead to Rugby. | | | |
| | Dec. 24th | Crew to Rugby. | | | |

Table 2 shows the number of different kinds of fields seen, and the numbers of them which contained rooks, starlings and lapwings. Such fields as corn, mowing grass and clover, and orchards and woods, in which no birds were noted, are omitted. In Table 3, the percentage of each kind of field containing the birds is shown in the first three columns; and the percentage of the total number of fields containing each species, which is found in the different kinds

of fields, is shown in the last three columns. It will be seen that, though by far the largest number of rooks are in the grass fields, the percentage of grass fields containing rooks is less than that of ploughed fields. In other words, they seem to prefer ploughed fields, but cannot find so many in which to feed. The same applies to lapwings. A high percentage of newly sown corn fields contained rooks, but as only 28 were seen, the numbers are not large enough to be significant. Their next preferences are for fields of stubble and cut hay. Starlings, on the other hand, feed almost exclusively in grass fields. They were not observed on ploughed land at all.

Table 2. *Total number of fields and birds seen.*

| Type of field | No. seen | No. with rooks | No. with starlings | No. with lapwings |
|---|---|---|---|---|
| Grass | 2541 | 260 | 83 | 51 |
| Rough grass | 681 | 31 | 9 | 3 |
| Rootcrops | 157 | 2 | — | 3 |
| Cut hay | 127 | 10 | 2 | — |
| Ploughed | 120 | 17 | — | 6 |
| Stubble | 91 | 9 | — | 1 |
| Cut corn | 58 | 3 | 2 | — |
| Allotments | 31 | 1 | — | — |
| New-sown corn | 28 | 3 | — | — |
| Total | 3834 | 336 | 96 | 64 |

Table 3. *Frequency of birds in different types of field.*

| Type of field | % with rooks | % with starlings | % with peewits | % of rooks in field | % of starlings in field | % of lapwings in field |
|---|---|---|---|---|---|---|
| Grass | 10·2 | 3·3 | 2·0 | 77·4 | 86·5 | 79·7 |
| Rough grass | 4·6 | 1·0 | 0·4 | 9·2 | 9·4 | 4·7 |
| Roots | 1·3 | — | 1·9 | 0·6 | — | 4·7 |
| Cut hay | 7·9 | 1·6 | — | 3·0 | 2·1 | — |
| Plough | 14·2 | — | 5·0 | 5·1 | — | 9·4 |
| Stubble | 9·9 | — | 1·1 | 2·7 | — | 1·6 |
| Cut corn | 5·2 | 3·5 | — | 0·9 | 2·1 | — |
| Allotments | 3·3 | — | — | 0·3 | — | — |
| New-sown corn | 10·7 | — | — | 0·9 | — | — |
| Total | 8·8 | 2·5 | 1·7 | | | |

In order to see whether season altered the feeding grounds, the results for the months October, December and January have been worked out, and compared with those for July, August and September (Table 4). Considerably more fields contained rooks during the winter months, 11·6 per cent. of the total, against 7·6 per cent. in the summer. The numbers with starlings were about the same, 3·0 and 2·2 per cent., while the number with lapwings was greater during the winter, 2·6 and 1·3 per cent. In the winter, more grass fields had rooks than in the summer, the ploughed fields were the same in both seasons, and there were many more cut hay and stubble fields containing rooks in the summer than in the winter. The starlings were occupying a greater percentage of the fields of cut corn than of the grass fields in the summer, while in the winter they were all in grass fields. Lapwings changed very little, but more were among root-crops in the winter than in the summer.

Table 4. *Frequencies of birds in different fields in summer and winter.*

| | Summer | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|
| Type of field | No. seen | % with rooks | % with starlings | % with lapwings | No. seen | % with rooks | % with starlings | % with lapwings |
| Grass | 1738 | 8·9 | 2·8 | 1·7 | 803 | 13·2 | 4·2 | 2·7 |
| Rough grass | 504 | 3·7 | 1·6 | 0·2 | 177 | 6·8 | 0·6 | 1·1 |
| Roots | 125 | 0·8 | — | 0·8 | 32 | 3·1 | — | 6·3 |
| Cut hay | 127 | 7·9 | 1·6 | — | 0 | – | — | — |
| Plough | 42 | 14·3 | — | 4·7 | 78 | 14·1 | — | 5·1 |
| Stubble | 54 | 13·0 | — | — | 37 | 5·4 | — | 2·7 |
| Cut corn | 58 | 6·2 | 3·4 | — | 0 | - | — | - |
| Allotments | 19 | — | — | — | 12 | 8·3 | — | — |
| New-sown corn | 0 | — | — | — | 28 | 10·7 | — | — |
| Total | 2667 | 7·6 | 2·2 | 1·3 | 1167 | 11·6 | 3·0 | 2·6 |

It is noteworthy that while rooks occurred in 8·8 per cent. of the fields, starlings were only in 2·5 per cent., and, as they have similar feeding habits, one would expect the smaller species to be the more numerous. They would probably have been shown to be so, if actual numbers of birds had been recorded. Rooks were often noticed alone or in small parties, whereas the starlings were always in flocks of at least 15–20 birds.

Table 5 shows the percentage of fields on different geological formations, which contained the birds. No very useful correlation is apparent. The highest percentage with rooks was on Devonian, and no other birds were seen. Cretaceous and Oolite had high percentages with rooks and starlings, while Trias, Cretaceous and Recent had the highest with lapwings.

Table 5. *The percentage of fields with birds on different geological formations.*

| Formation | No. of fields seen | % with rooks | % with starlings | % with lapwings |
|---|---|---|---|---|
| Trias | 2144 | 8·1 | 2·8 | 2·5 |
| Cretaceous | 377 | 12·2 | 3·7 | 2·1 |
| Oolite | 375 | 12·8 | 4·0 | 0·5 |
| Lias | 330 | 11·5 | 2·2 | 0·3 |
| Devonian | 139 | 13·0 | 0·0 | 0·0 |
| Recent | 138 | 3·6 | 1·5 | 2·2 |
| Carboniferous limestone | 95 | 2·1 | 2·1 | 0·0 |
| Eocene | 63 | 7·9 | 1·6 | 1·6 |
| Permian limestone | 58 | 3·5 | 0·0 | 0·0 |
| Coal measures | 50 | 6·0 | 0·0 | 0·0 |
| Total | 3769 | 8·9 | 2·6 | 1·7 |

## SUMMARY.

Observations were made from the train, on birds occurring in different kinds of fields, between the months of July and January. Out of 2834 fields, 8·8 per cent. contained rooks, 2·5 per cent. starlings and 1·7 per cent. lapwings. More fields contained rooks and lapwings during the winter than during the summer months. The numbers with starlings were about the same. Certain changes in feeding grounds were noticeable between the two seasons. The different geological formations did not appear to have any important effect on the feeding grounds of these birds, or on their distribution.

# THE EFFECT OF TEMPERATURE AND HUMIDITY UPON THE EGGS OF THE BUG, *RHODNIUS PROLIXUS* (HETEROPTERA, REDUVIIDAE)

By NANCY CLARK.

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(*With 2 Figures in the Text.*)

## 1. Introduction.

The present work is an account of investigations carried out upon the reactions of the eggs of *Rhodnius prolixus* Stål. to varying conditions of temperature and humidity, with a view to studying the vital limits of the egg, factors affecting the duration of the egg stage, and the percentage hatch of the eggs obtainable under various controlled conditions. *Rhodnius* is a blood-sucking bug, native to S. America. In captivity it can be fed on rabbits. A general account of its biology may be found in Buxton (1930).

## 2. Material.

The eggs used in the experiments were obtained from a culture of *Rhodnius* bred at 23–24° C., and at unknown but fairly constant humidity, which was maintained by keeping open pans of water in the incubator. In every experiment eggs were used that had been laid within the preceding 24 hours, not necessarily of the same parents. Infertile eggs could sometimes be distinguished within two or three days, owing to the retention of a yellowish tinge (fertile eggs becoming pink). By the end of the experiment it was always possible to recognise infertile eggs at a glance by colour, and the lack of eyespot or signs of development in the embryo, which is visible through the chorion.

After preliminary experiments, it was found that the percentage of infertile eggs (see definition of terms in Norris, 1933, p. 906) was very low indeed (3·3 per cent. of 1925 eggs), and further, that the eggs reacted to conditions in a very constant manner, showing little individual variation. Therefore in each experiment only ten to twenty eggs were used. Experiments at each combination of temperature and humidity were repeated three or four times and, where the results were at variance, were again repeated, using larger numbers of eggs (see Table). Controls (i.e. batches of eggs obtained at the same time as those used in the experiment) were maintained at 25° C. and 70 per cent. R.H. A record of the number of control eggs hatching showed that the percentage infertility was quite unaffected by temperature and humidity. In each experiment, therefore, any infertile eggs were excluded.

### 3. METHOD OF CONTROLLING TEMPERATURE.

Constant temperatures from 24 to 36° C. and 12° C. were obtained by using Hearson's gas or electric incubators. More difficulty was experienced in maintaining constant temperatures at 15–24° C., and occasional variations occurred within 2–3° C. A temperature of 15–17° C. was obtained by placing the experimental tubes in jars inverted in tap water flowing at a constant rate. A temperature of 20–23° C. was obtained by means of a desiccator packed in a tin of asbestos wool and left in the laboratory.

### 4. METHOD OF CONTROLLING HUMIDITY.

It was decided to work with aqueous solutions of sulphuric acid of known specific gravity producing different relative humidities, which are convertible, when necessary, to saturation deficiencies. The solutions were made up in accordance with Wilson's tables (1921) correct for 15° C. with a Beaumé hydrometer. The error introduced through using the same solutions at 35° C. is of no great practical importance, as has been shown by Buxton (1931 *b*).

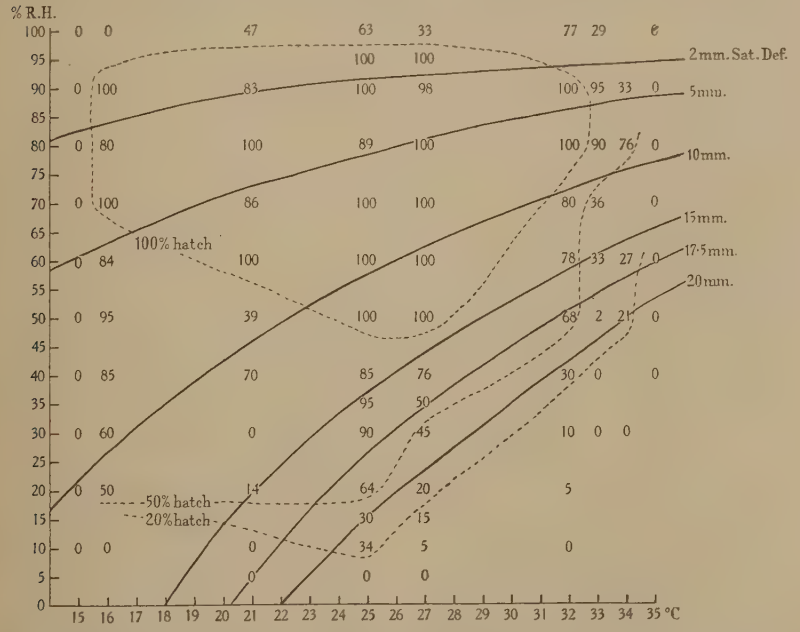


Fig. 1. Relation of percentage hatch of *Rhodnius* eggs to temperature and humidity. Abscissa = ° C. Ordinate = percentage R.H. A figure representing percentage hatch is placed at a point corresponding to each combination of temperature and humidity tested. Lines have been added showing (*a*) 100, 50 and 20 per cent. hatch and (*b*) saturation deficits of 2, 5, 10, 15, 17·5 and 20 mm. of mercury.

The eggs were subjected to the constant relative humidities by placing them in $1 \times \frac{1}{2}$ in. glass tubes covered with muslin and suspended in $3 \times 1$ in. glass tubes containing approximately 1 in. of sulphuric acid solution. The outer tubes were closed with waxed corks to prevent gaseous diffusion. It was possible to see the eggs through the tubes, which were not opened until the conclusion of the experiment. At high temperatures and high humidities fungus attack spoilt several experiments.

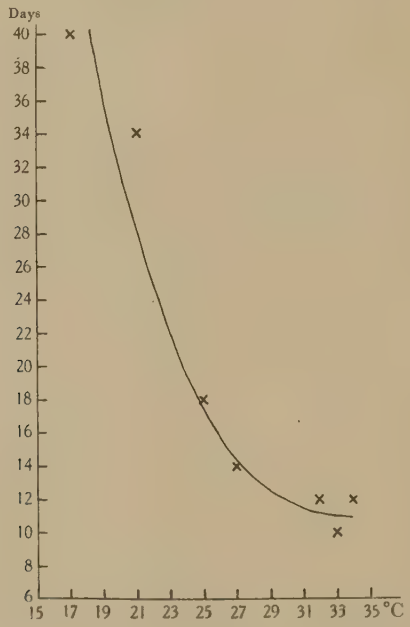


Fig. 2. Duration of egg stage in days at various temperatures ° C.

### 5. Effect of temperature and relative humidity upon the duration of the egg stage.

Temperature is the dominant factor in the control of the duration of the egg stage. At 34° C. development takes 12 days, at 33° C. 10 days, at 32° C. 12 days, at 27° C. 14 days, at 25° C. 18 days, at 21° C. 34 days, and at 17° C. as long as 40 days. The relation between temperature and duration of development is shown graphically in Fig. 2. (The number of eggs tested at each temperature may be obtained from the table by adding together the eggs incubated at all humidities (except 100 per cent.).) At any one temperature, the only difference that can be detected in the duration of the egg stage is a lag of 12–24 hours in completely saturated air. This lag is found at all tem-

peratures for the egg of *Rhodnius*. Zwölfer (1931) records a similar retardation in the development of *Panolis flammea* in saturated air.

*Table of experimental results.*

In the table the experiments are arranged under temperatures; the first figure is the percentage relative humidity; the next, a figure without brackets, is the number of eggs used in the experiment; the third figure, in brackets, is the number of eggs which hatched; the fourth figure, included where necessary, is the average percentage hatch.

16° C. At all humidities there is complete mortality and no signs of development in the embryo.

15–17° C. 100 % 20 (0); 90 % 10 (10); 80 % 20 (16); 70 % 10 (10); 60 % 19 (16) 84 %; 50 % 20 (19); 40 % 20 (12); 20 % 20 (10); 10 % 20 (0).

21–23° C. 100 % 35 (13) 37 %; 90 % 23 (19) 83 %; 80 % 15 (15); 70 % 35 (30) 86 %; 60 % 8 (8); 50 % 59 (23) 39 %; 40 % 62 (43) 70 %; 30 % 20 (0); 20 % 21 (3) 14 %; 10 % 10 (0); 5 % 20 (0).

25° C. 100 % 60 (38) 63 %; 95 % 20 (20); 90 % 19 (19); 80 % 29 (26) 89 %; 70 % 39 (39); 60 % 10 (10); 50 % 38 (38); 40 % 40 (34) 85 %; 35 % 20 (19); 30 % 20 (18); 20 % 55 (35) 64 %; 15 % 20 (6); 10 % 38 (11) 34 %; 5 % 10 (0).

27° C. 100 % 58 (19) 33 %; 95 % 19 (19) 90 % 43 (42) 98 %; 80 % 20 (20); 70 % 38 (38); 60 % 20 (20); 50 % 30 (30); 40 % 29 (22) 76 %; 35 % 48 (24); 30 % 38 (18) 45 %; 20 % 40 (8) 20 %; 15 % 20 (3); 10 % 20 (0); 5 % 10 (0).

32° C. 100 % 30 (23) 77 %; 90 % 19 (19); 80 % 19 (19); 70 % 20 (16); 60 % 37 (29) 78 %; 50 % 28 (19) 68 %; 40 % 30 (9); 30 % 18 (2) 10 %; 10 % 20 (0).

33° C. 100 % 38 (11) 29 %; 90 % 20 (19); 80 % 10 (9); 70 % 39 (14) 36 %; 60 % 30 (10); 50 % 40 (1); 40 % 10 (0); 30 % 10 (0).

34° C. 90 % 30 (10); 80 % 25 (19) 76 %; 60 % 30 (5) 17 %; 50 % 34 (7) 21 %; 30 % 10 (0); 20 % 20 (0).

35 and 36° C. At all humidities there is no hatch, but the embryo develops completely.

### 6. Effect of temperature and humidity upon the percentage hatch of eggs (see Fig. 1).

The upper vital temperature limit beyond which no hatch can be obtained is 34° C. At 35 and 36° C. and at relative humidities greater than 70 per cent. the embryos develop completely within the chorion but fail to hatch. It appears, therefore, that the upper vital limit is determined by some physical effect of heat upon the chorion rather than upon the developing embryo. The chorion appears to become hard, so that the cap cannot be forced off by the embryo. Alternatively, there may be a lack of turgidity in the embryo. The lower vital limit has not been determined with complete accuracy, owing to the difficulty of maintaining the necessary temperatures constant over a period of 5–6 weeks. At 12° C. no development whatsoever can be detected in the embryo. At 15° C. (possibly falling to 13° C.) no hatch is obtained, at 16° C. (possibly rising to 17–18° C.) hatching occurs, at 17° C. over a wide range of humidities a comparatively high percentage is obtained. The lower vital limit, therefore, lies between 13 and 16° C. It is of interest to note that the lower vital limit is dependent not upon the physical condition of the chorion, but upon cessation of development in the embryo itself.

From 17 to 33° C. humidity becomes the dominant factor in percentage hatch. Given suitable humidity conditions, a high percentage hatch can be obtained at any temperature. At all temperatures, relative humidities from

70 to 90 per cent. lie within the optimum developmental area. Complete saturation causes a considerable mortality amongst the eggs: this appears to be a general rule for insect eggs, having been recorded by Zwölfer (1931) for *Panolis flammea*, Parker (1930) for *Sitona lineata*, von Maercks (1933) for *Habrobracon*.

As a general rule, decrease in relative humidity causes a decrease in the percentage hatch, the extent of which is dependent upon temperature. At 17° C. there is total mortality at 10 per cent. R.H. and a hatch of less than 80 per cent. from 10 to 30 per cent. R.H. At 24° C. 100 per cent. hatch is obtained over a wide range of humidity, i.e. from 95 to 50 per cent. R.H. The percentage hatch does not fall off seriously until 20 per cent. R.H., and some eggs are able to hatch at 10 per cent. R.H. At a temperature of 32° C. a high percentage is obtained over a wide range of humidity, but the percentage falls more rapidly with decreasing humidity than at 25° C. Above 30° C. relative humidity has a marked effect in narrowing the range within which eggs can hatch.

The effect of decreased relative humidity appears in all cases to be a physical effect upon the egg shell as the embryo within is completely developed. It is probable that external conditions of relative humidity have little effect upon the embryo itself and only become important factors immediately before hatching. This evidence supports the opinions put forward by Buxton (1931*b*) in his review of the effects of temperature and humidity upon terrestrial insects.

### 7. Saturation deficiency as a limiting factor.

In the same paper, Buxton (also in 1931*a*) suggested that saturation deficiency was of greater significance than relative humidity in many insect problems. Using Parker's figures (1929) he showed that in *Melanoplus mexicanus* percentage hatch has a closer relation to saturation deficiency than to relative humidity. On the other hand, when the results of Bodenheimer (1929) on *Schisticerca gregaria* eggs, Zwölfer (1931) on *Panolis flammea* eggs, and von Maercks (1933) on *Habrobracon* eggs are plotted and saturation deficiency lines are drawn, no closer relation emerges between these lines and percentage hatch than can be shown for relative humidity. In *Rhodnius* eggs, within the optimum temperature range, the lines of 20 and 17·5 mm. saturation deficiency lie near the limits of 20 and 50 per cent. hatch respectively. No direct relation can be seen between relative humidity and percentage hatch.

### 8. Summary.

1. Experiments were set up to study the effect of temperature and humidity upon (*a*) duration of the egg stage, (*b*) percentage hatch in the eggs of *Rhodnius prolixus*.

2. Eggs laid within the preceding 24 hours were used in the experiments.

3. Temperature controls the duration of the egg stage, except that at complete saturation there is a small retardation in development at all temperatures.

4. Above 34° C. no embryos hatch, though they may complete development at 36° C.

5. 100 per cent. hatch is obtained over a wide range of temperature and humidity conditions.

6. The percentage hatch is decreased at all temperatures by (*a*) decreasing relative humidity below a certain minimum which rises with temperature, (*b*) complete saturation of the atmosphere.

My thanks are due to Prof. J. W. Munro in whose department this work was done and to Dr O. W. Richards for his help and advice.

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# A PRELIMINARY INVESTIGATION ON THE ECOLOGY OF THE COMMON MOLE (*TALPA EUROPEA*)

By JOHN FORD.

In the winter and spring of 1933-4 the writer undertook an investigation of certain mole colonies near Oxford with a view to establishing the approximate density of mole populations and to finding a means of conducting a census on a larger scale. The investigations could not be completed in the time available, but certain results are worth noting.

*Trapping.* Mole-infested areas were trapped at Sandford, at Barton and in Port Meadow. Scissor traps were used and set in rows, four in each row, the two most distant traps being not more than 10 yards apart. Four such rows were used, either parallel or at right angles to one another, in such a manner that one trap, at least, lay in every main run within an area of about 400 square yards. Each day the traps were moved to a fresh area overlapping that of the previous day. When, after two days' trapping, no more moles were taken from a colony and no new workings could be seen, the traps were moved to a fresh colony in the same field. In all, areas amounting to 5150 square yards were thoroughly trapped, which, together, yielded nineteen animals, giving a density of 18 per acre. The soil in these areas is heavy, with a large admixture of clay. In a light loam overlying limestone, near Bristol, the same estimate, of 18 per acre, for mole population density was made by Mr A. W. Ling (*in litt.*; see also Ling, MacEachern and Read, 1930).

*The sex ratio in moles.* Of the 19 moles trapped, 13 were males and 6 females. Lionel Adams, however, is of the opinion that the sex ration is 1 : 1 (Adams, L. 1903). The discrepancy in the present trapping may be accounted for by migrations of females, for nesting purposes, to woodlands. This is the reliable opinion of a professional mole-catcher (*per* G. H. Bates, Norfolk Department of Agricultural Education). Evidence in support of a 2 : 1 ratio was obtained on Ilsley Down, Berks, where, of 16 moles picked up from shallow runs by a dog, in the course of a single morning, 11 were males and 5 females. All were young animals, the males with immature testes (length 2·5-3 mm.) and the females with very small uteri. The mean weight of the males was 75 gm., and of the females 68 gm. (The mean weight of adult males trapped near Oxford was 98 gm. and of females 82 gm.) The animals on Ilsley Down were taken in early May and had evidently only recently left the nests. As yet there is insufficient evidence to establish the real sex ratio.

*Fortresses.* These are probably built only by males; they are fully described by Adams (1903). On the Ilsley Down 17, showing signs of recent working and containing nests, were counted in an area of about nine acres. Fortresses are

not communal and, clearly, all the males in this heavily infested area cannot have made fortresses. It is probable that the females and young males are more or less social, while the old males are solitary (Ling, and others, 1930), and it is here suggested that it is only the old males which build fortresses at all. In some districts, however, fortresses and large mounds are built more frequently, as in the Fens, where they may serve for the avoidance of underlying water.

*Food.* The stomach contents of the Oxford moles consisted almost entirely of worms (Lumbricidae). On Ilsley Down, Berks., where there is a light shallow soil overlying chalk, there are very few worms and stomach contents were over 90 per cent. composed of insect larvae and centipedes (Myriopoda, Notophilidae).

*Influence of moles on vegetation.* Ten quadrats, each of 1 sq. yard, were examined in a mole-infested area on Ilsley Down and the number of thistles (*Cirsium ? pratense* Huds.) in each was counted. The same process was repeated in an adjacent area kept free of moles by trapping. The number of thistles per square yard of mole-infested ground was 6·9 and in the mole-free area 0·7. This survey was suggested to me by Mr G. H. Bates who reported that *Cirsium arvense* Robs. was influenced by the presence or absence of mole heaps, as it is a coloniser of bare ground, and is thus encouraged to grow where mole heaps kill the grass. Regarding most plants, however, moles cause a decrease in population. It was estimated that approximately 25 per cent. of the ground, where moles were present, on Ilsley Down, was devoid of vegetation owing to earth thrown up by these animals.

Acknowledgments and thanks are due to Messrs Lionel Adams, A. W. Ling, G. H. Bates and A. D. Middleton for help and advice.

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# RHODESIAN ASILIDAE (DIPTERA) AND THEIR PREY COLLECTED BY MR C. F. M. SWYNNERTON

By B. M. HOBBY.

(*From the Hope Department, University Museum, Oxford.*)

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## 1. Foreword and acknowledgments.

This paper is an account of a collection of nearly 500 Asilidae taken with their prey by Mr C. F. M. Swynnerton during December, 1911, and the first quarter of the succeeding year, at 3800–3900 ft. on Mount Chirinda, S.E. Rhodesia, and presented by him to the Hope Department, University Museum, Oxford. The study of this collection was initiated by Sir Edward Poulton and the late Col. J. W. Yerbury in 1914, but had to be discontinued owing to the outbreak of the War. At the suggestion of Prof. Poulton the work was recently resumed by the writer as part of a general investigation of the feeding habits and prey of predacious insects.

Some of the determinations date from the initial studies of 1914, and are due to Mr G. J. Arrow (Coleoptera), Major E. E. Austen (Diptera), the late Messrs W. L. Distant (Hemiptera) and C. J. Gahan (Coleoptera), Sir George Hampson (Heterocera), and Mr G. Meade-Waldo (Hymenoptera). The greater part of the collection has been determined recently, the Asilidae (with the exception of the species of *Neolaparus*), Orthoptera and Rhopalocera by the writer, and the remaining groups by Mr R. B. Benson (Hymenoptera), Mr W. E. China (Hemiptera), Dr C. Ferrière (Ichneumonoidea), Mr D. E. Kimmins (Mecoptera, Neuroptera and Odonata), and Messrs H. Stringer and W. H. T. Tams (Heterocera).

I desire to express my deep indebtedness and very sincere gratitude to the above-mentioned entomologists for the kind help always so freely given, and also to Mr B. P. Uvarov who gave me much valuable help while studying the Orthoptera in the British Museum (Natural History) and also verified my determinations; to the late Dr F. A. Dixey, Dr H. Eltringham and Sir Edward Poulton for similar assistance with the Rhopalocera; to Mr C. F. M. Swynnerton for the description of Mount Chirinda which he wrote at my request in June, 1933; to Dr J. Burtt Davy for advice on the names of plants; to Prof. G. D. H. Carpenter and Dr O. W. Richards for reading the manuscript and suggesting improvements; and to Comm. J. J. Walker for much kind help and also assistance with the proofs.

I also wish to acknowledge my indebtedness to the important papers of Poulton (1907), Melin (1923), and Whitfield (1925), which have been most useful in all stages of the work, and have suggested convenient methods for the presentation of results.

I began the investigation as a Research Student of the Department of Scientific and Industrial Research and it has been prepared for publication during the tenure of a Junior Research Fellowship at the Queen's College, Oxford.

## 2. Introduction.

The following remarks are largely based upon Melin's (1923) and Whitfield's (1925) studies of European species.

### (*a*) *Method of feeding.*

Asilidae are predacious throughout their adult life, and take no food other than living insects. Immediately an insect is captured, the proboscis is plunged into its tissues (usually at the back of the head) and a fluid injected which causes death almost instantaneously. This poison is secreted by a pair of thoracic glands opening into the hypopharynx; there is also a pair of labial glands producing secretions which dilute the body fluids of the prey and dissolve the more solid parts of its internal anatomy.

### (*b*) *Method of hunting.*

Many species of Asiline robber-flies sit about on the bare ground, stones, logs and other exposed situations fairly near the ground which give them an uninterrupted view of passing insects. Others seek more elevated positions and keep watch from the leaves or bare branches of trees, sometimes at a height of several metres from the ground. These capture their prey on the wing by means of a "capture-dart"; the Leptogasterinae, however, not only track down their prey in the course of longer flights, but also attack resting insects, a similar method of hunting being sometimes adopted by species of the Dasypogonine genus *Dioctria*. Asilidae adopting these various methods of

hunting come into contact with quite different populations and secure different species as prey.

(*c*) *Morphological adaptations.*

The capture of swiftly moving insects is dependent, above all, upon corresponding swiftness of flight and great keenness of vision, two factors in which the different species show considerable variation. Next must be considered adaptation of the legs for capture of prey, for although the tarsi of all Asilidae are provided with strong bristles, the bristles and hairs of the tibiae, femora and coxae show great variation in number, position and development. As Melin has pointed out, the longer and stronger the legs, and the coarser the bristles, the stronger will be the apparatus of capture and the larger the prey that can be caught and successfully retained. If, however, the legs have a dense covering of long bristles or hairs, quite small insects can be captured. Some predators, therefore, capture only small insects, others large ones, while a third kind catches both large and small prey. The mouth-parts of Asilidae are adapted for piercing, the labium forming a sheath enclosing the maxillae and hypopharynx, and, with the maxillae and epipharynx, acting as a guide for the lancet-like protractile hypopharynx. Insects with a very hard integument may be killed only if the hypopharynx is able to pierce hard chitin; this depends not only on the actual strength of the hypopharynx, but also upon the support given to it by the maxillae and the labium. For these reasons many Asilidae are able to capture weakly chitinised insects only, but those with a strongly developed proboscis are able to capture insects having a hard or a soft integument.

(*d*) *Preferential selection.*

Specialisation of the feeding habits of Asilidae is never so highly developed that only insects of a single order or family are captured. Incipient preferential selection presumably occurs in *Dioctria*, the species of which often capture Ichneumonidae, a group rarely observed as prey of other Asilidae. Other instances are known in which a considerable proportion of the prey consists of insects of a certain family or order (several are recorded in this paper), but in these it is not always possible to say whether such a result is due to abundance of these species in particular associations, to morphological adaptation, or to preferential selection.

## 3. Locality where the Asilidae were collected.

"Mount Selinda", the map locality in Southern Rhodesia in which the collection was made, is an extensive hill, down-like in form and with valleys and streams running down from it. It rises to eight hundred or a thousand feet above the dissected plateau land to the north, and on its east and west sides falls to greater depths in the valleys of the Zona and Umswirizwi rivers. The steep north face of the hill consists of exposed shale and is clothed with

savannah wooding of *Uapaca kirkiana* Müll. Arg., *Isoberlinia globiflora*[1] (Benth.) Hutch., and *Brachystegia* of more than one species. On the upper surface of the hill are two areas of loose grey soil derived from sandstone on which *Parinarium curatellaefolium* Planch. is the main woody species, but the bulk of the top of the hill is composed of a dolerite cap, productive of a red loam soil.

On its top are two areas of exceptionally fine rain forest; one of these forests, "Chirinda", covers 1200 acres, the other, "Chipeti", 200 acres. The rest of the hill, whether wooded or open, is grassy and grazed closely by cattle. The red loam soil supports an exceptionally rich growth of grass and herbaceous climbers (*Dioscorea*, *Mucuna*, etc.), with *Acacia natalitia* E. Mey. groves on ground from which rain forest has disappeared recently, and *Pterocarpus rotundifolius*[2] (Sond.) Druce, mostly burned down but regenerating, where the old forest humus has largely deserted the soil through a longer period of exposure. The vegetation of the outskirts of the forest was particularly rank, but a long stretch was cleared.

The collector's homestead was 3900 ft. above sea-level and within 80 yards of the northern outskirts of the Chirinda rain forest. His coffee plantations, timber belts, orchards and maize field covered a considerable area of the red doleritic soil, although his roads and some cultivation ran out on to the sandier area. The pastures were on the dolerite, sandstone and shale alike. Red cultivated soil existed between the rows of coffee and fruit trees. Weeds grew up fast between weedings in the rains, but not in the later dry season when the Asilidae were most in evidence. It was in these plantings and on their paths, and in the short-grassed pastures, shooting young and green before the advent of the rains, that the Asilidae for the most part were caught. They settled on the bare ground or on twigs—especially bare twigs; *Alcimus setifemoratus*[3] Hobby settled mainly on the ground.

The rainfall of the locality varied from 60 to 80 in. and in one year reached 120 in. The dry season was well marked with, normally, one rain in May, and cloud and drizzle in July. August and September were dry and increasingly windy, and October, till the first thunderstorms fell, particularly hot and dry.

### 4. Structural adaptations and habitat of the species of Asilidae, and nature of their prey.

*Microstylum ustulatum*[4] Engel.

A large robust species ranging in size from 25 to 30 mm. The legs are adapted for the capture of large insects inasmuch as the tibiae and femora have numerous long strong bristles, but not such a well-developed covering of hair. The proboscis is about 4 mm. in length and about as long as the head; the strong hypopharynx is well adapted to pierce hard chitin.

[1] Also known as *Berlinia globiflora* (Benth.) Hutch. and Burtt Davy.
[2] Also known as *Pterocarpus sericeus* Benth.
[3] Formerly confused with *Alcimus rubiginosus* Gerst. (see Hobby, 1934*a*).
[4] Determined by comparison with paratype so named in the British Museum (Natural History).

20 examples are recorded with prey; of these 18 were from pasture, and two from coffee plantations. Relative to the size of the Asilid captor, the prey (8 Orthoptera, 4 Diptera, 4 Hymenoptera, 2 Coleoptera and 2 Hemiptera) consists of large to very large insects having a fairly resistant or very hard integument; all exceed 10 mm. in length, three being larger than the predator.

*Microstylum nigrostriatum* Hobby.

A more slender species, 20–22 mm. in length. The legs have a scanty covering of short, pubescence and rather short, weak bristles and are best adapted for the capture of medium-sized insects. The proboscis is a little longer than the head which is about 3·25 mm. in length; relatively to the size of the Asilid it is rather strong. The nine individuals taken with prey were all from pastures. The prey (3 Diptera, 3 Orthoptera, 2 Coleoptera and 1 Hemiptera) consists of medium- to fairly large-sized insects (8–25 mm. in length). Of these, only the two Cerambycidae have a very hard integument, but all the remainder have a fairly tough exoskeleton.

*Neolaparus lugubris* Becker and *Neolaparus* spp. ♂ and ♀.

As only five specimens of this genus were taken with prey and these represent three distinct species, it seems best to deal with them collectively. The three species are about 24 mm. in length and best adapted for the capture of medium-sized insects, although the better covering of hairs on the posterior tibiae should enable them to seize and hold much smaller insects than either of the two species discussed above. The proboscis is approximately equal in length to the head, but is only about 2·75 mm. long and probably not so effective as that of the last species. The prey consists of 2 Coleoptera, 1 Hymenoptera, 1 Mecoptera and 1 Lepidoptera. The beetle and wasp have hard integuments, but the moth and the *Bittacus* are less well chitinised; both the *Bittacus* and the moth are about the same size as the captor, the wasp is rather smaller, and the beetles quite small (3–5 mm.).

*Laxenecera albicincta* Loew.

A sexually dimorphic species, the females originally being known as *Laxenecera zonata* Loew. About 17 mm. in length, but rather stoutly built; the legs short, with very powerful femora and a dense covering of hairs and bristles. Proboscis stout; a little shorter than the head; about 2 mm. in length. The five specimens obtained with prey were all from pasture. The prey (3 Orthoptera, 1 Diptera, and 1 Hymenoptera) consists of insects with a fairly hard integument not differing greatly from the captor in size.

*Proagonistes rufibarbis*[1] Fab.

A large and powerful species ranging in length from 32–36 mm. Legs well provided with bristles; hairs relatively much shorter than in *Laphria albicincta*,

[1] All four specimens agree with Bromley's (1930*a*) account of *P. athletes* Speiser, but Engel (1932) considers *athletes* a synonym of *rufibarbis*. Since the above was written Bromley, 1935, *Ann. Mag. Nat. Hist.* (10) 15, 398–9, suggests that it would be better to retain the name *athletes* until more conclusive evidence is obtained that the two forms are varieties of the same species.

the only other Laphriine species in the collection. The exceedingly strong proboscis is about 5·5 mm. long and slightly exceeds the head in length. Its much swollen base is suggestive of well developed muscles or of enlarged glands, while its upwardly curved structure may be an adaptation for the piercing of hard chitin as is suggested by Melin (1923) as a possible explanation of the similarly shaped organ in *Dioctria* and *Pamponerus*.

Of the four examples obtained with prey, two are from coffee plantations; the habitat of the others is unrecorded. The prey consists of 3 formidable Aculeate Hymenoptera and 1 moth; all are medium-sized insects relative to the captor. The Aculeates have a hard integument, the moth a much softer one. The few previously published records of the prey of *Proagonistes* include more Hymenoptera than insects of other orders, but much more information is required before one can safely suggest a specialised attack on the Aculeata.

*Promachus aequalis*[1] Loew.

A stoutly built species, 17–21 mm. in length, with well developed bristles and long hairs on the femora and tibiae. The proboscis is about 2·75 mm. long and a little shorter than the head. 20 specimens are recorded with prey, of these nineteen are from pasture, and one from a coffee plantation. The prey (7 Hymenoptera, 6 Orthoptera, 3 Coleoptera, 3 Diptera, and 1 Hemiptera) consists almost entirely of relatively large insects with a tough or hard integument, but includes a few of medium size.

*Promachus* sp.? *robertii*[1] Macq.

Similar in structure to *Promachus aequalis*, but slightly larger (21 mm.) and more stoutly built. The proboscis is about 3·5 mm. in length while the head is a little longer. The only recorded prey is a medium-sized Hymenopteron with a hard integument.

*Philodicus swynnertoni* Hobby.

A robust species 22–25 mm. in length. The legs are clothed with short appressed hairs and rows of bristles; they are not well adapted for the capture of very small prey. The proboscis is about 3 mm. in length, the head a little longer. The 117 examples in the collection were all from pasture. The prey includes 45 Orthoptera, 32 Hymenoptera, 20 Diptera, 13 Hemiptera, 5 Coleoptera, 1 Lepidoptera and 1 Mecoptera. On the whole these are insects with a hard or tough integument, half as large or as large as the captor.

Although the proportion of Orthopterous prey is considerable (39 per cent.) this cannot be taken as evidence for preferential selection for this predator not only occurs in an ecological association where grasshoppers are very abundant, but also (if its habits conform to those of the majority of Asiline robber-flies) adopts a method of hunting which brings it frequently into contact with insects

[1] In a paper shortly to be published elsewhere it is shown that *P. aequalis* Loew is distinct from *P. fasciatus* Fab. and that the synonymy given by C. Kertész (1909) is erroneous. The status of *P. robertii* Macq. is also discussed.

alighting on the ground. Furthermore, as pointed out above, this insect is not well adapted for the capture of small insects, although able to retain successfully larger insects, including grasshoppers. These three factors seem sufficient to account for the large proportion of Orthoptera. Should preferential selection be a fourth important factor, a much higher percentage of Acridian prey might be expected.

The Hymenopterous prey includes more bees than wasps, a result possibly not unconnected with the presence of flowering plants in the vicinity. The Diptera, as in the general list for all species, mainly comprise Asilidae and Bombyliidae. The Orthoptera, with these two orders, account for nearly five-sixths of the prey, the Hemiptera, Coleoptera, Lepidoptera and Mecoptera being apparently of little importance.

*Philodicus nigripes* Ricardo.

Morphologically very similar to *Philodicus swynnertoni*, but smaller (16–21 mm.) and more slender. The proboscis is only about 1·75 mm. long and the legs are not adapted for the capture of small insects. The 33 specimens with prey were all from pasture, the prey being 10 Hymenoptera, 8 Orthoptera, 7 Diptera, 5 Hemiptera, 2 Coleoptera and 1 Lepidoptera. These numbers are insufficient to be compared safely with the prey of the last species; but it may be noted that the Hymenoptera, Orthoptera and Diptera collectively form the bulk of the prey of both species of *Philodicus*. Many species are common as prey to both these Asilidae, but on the whole the prey of *Philodicus nigripes* is rather smaller than that of *Philodicus swynnertoni*.

*Alcimus setifemoratus* Hobby.

A large robust species, 25–33 mm. in length. The proboscis is 3 mm. in length and about three-quarters as long as the head. The long, strong legs have a covering of long, erect, fine hairs on the ventral surfaces of the femora and tibiae; the tibiae have strong bristles and there are also rows of bristles on the intermediate and posterior femora in both sexes and on the anterior femora of the female, but not of the male. Of 231 prey, 135 were from coffee plantations, 75 from pasture, 2 from forest and 19 from unrecorded habitats. On the whole the prey consists of medium- to large-sized insects with a fairly tough integument; it comprises 122 Orthoptera, 52 Lepidoptera, 25 Diptera, 11 Hymenoptera, 9 Hemiptera, 5 Coleoptera, 3 Neuroptera, and 2 Odonata; one specimen not included in this list was lost, but three butterflies picked up dead in situations much favoured by *Alcimus setifemoratus*, and most probably the prey of this species, are included.

As in the case of *Philodicus swynnertoni*, the large proportion of Orthoptera (53 per cent.) is most probably due to local abundance, method of hunting, and structural adaptation for the capture of large-sized insects rather than to preferential selection. Next in numbers come the Lepidoptera with 52 records representing 23 per cent. of the prey. Of these, 9 are moths, the remainder

butterflies. Since the collection as a whole contains only four further instances of Lepidopterous prey it seems most probable that *Alcimus setifemoratus* exercises preferential selection and specially attacks this order. Diptera, represented by 25 specimens (11 per cent.), all but two of which are Asilidae, come next in numbers, while Hymenoptera (which formed a considerable proportion of the prey of *Philodicus*) are fourth on the list with only 4 per cent. The remaining orders are not of great importance as prey, but include the only Neuroptera, Odonata, and Isoptera in the collection.

*Neolophonotus rhodesiensis* Hobby.

A medium-sized species (15–19 mm. in length) having legs well provided with long stiff hairs and rows of bristles which are very strongly developed on the ventral surfaces of the posterior femora. The proboscis is about 2 mm. in length and only about two-thirds as long as the head. The 39 specimens with prey were all from pasture. The prey consists of 17 Hymenoptera, 9 Orthoptera, 8 Diptera, 2 Coleoptera and 2 Hemiptera; in one instance the prey is missing. On the whole the insects captured do not differ greatly in size from the captor and have a rather tough or hard integument; the single Syrphid is one of the smallest and most weakly chitinised insects captured. Rather more than a third of the prey are bees, but the material is obviously insufficient to determine whether this is significant or not.

*Merogymnus nigroflavipes* Hobby.

A medium-sized species (18–20 mm. in length) without such a dense covering of hairs on the legs as in *Neolophonotus rhodesiensis*, but not unlike this species as regards development of bristles. The proboscis is only about 1·75 mm. in length, the head being about a millimetre longer. The 12 specimens obtained with prey were all from pasture. The prey consists of 6 Orthoptera, 2 Hymenoptera, 2 Diptera and 2 Hemiptera, and are mostly insects having a tough integument, of about the same size as the captor.

*Synolcus aurulentus* Engel.

A smallish species (16 mm. in length) with moderate development of bristles and few hairs. The proboscis is about 1·5 mm., and the head about 2·0 mm., in length. The only prey is an immature Orthopteron taken in pasture.

### 5. Relative frequency of attack by males and females.

In previous investigations on the prey of Asilidae, females have been found with prey more often than males. In the Swynnerton collection males and females occur in approximately equal numbers, but this result is largely due to an excess of forty male *Alcimus setifemoratus*, five *Philodicus swynnertoni*, and three *Neolophonotus rhodesiensis*.

Apart from these three instances the remaining species show the same predominance of females noted above.

Table 1. *Relative frequency of attack by males and females.*

| Rhodesian Asilidae | Number taken with prey | | | | | |
|---|---|---|---|---|---|---|
| | Total for each species | | | Total for each subfamily | | |
| DASYPOGONINAE | ♂ | ♀ | Total | ♂ | ♀ | Total |
| *M. ustulatum* Engel | 2 | 18 | 20 | | | |
| *M. nigrostriatum* Hobby | 1 | 8 | 9 | | | |
| *N. lugubris* Becker | — | 3 | 3 | | | |
| *Neolaparus* sp. J. | — | 1 | 1 | | | |
| *Neolaparus* sp. Q. | — | 1 | 1 | 3 | 31 | 34 |
| LAPHRIINAE | | | | | | |
| *L. albicincta* Loew. | 2 | 3 | 5 | | | |
| *P. rufibarbis* Fab. | 1 | 3 | 4 | 3 | 6 | 9 |
| ASILINAE | | | | | | |
| *P. aequalis* Loew. | 8 | 12 | 20 | | | |
| *P.* sp. ? *robertii* Macq. | — | 1 | 1 | | | |
| *P. swynnertoni* Hobby | 61 | 56 | 117 | | | |
| *P. nigripes* Ricardo | 12 | 21 | 33 | | | |
| *A. setifemoratus* Hobby | 133 | 93 | 226 | | | |
| *N. rhodesiensis* Hobby | 21 | 18 | 39 | | | |
| *M. nigroflavipes* Hobby | 2 | 10 | 12 | | | |
| *S. aurulentus* Engel. | — | 1 | 1 | | | |
| Asilinae sp. indet. | — | 1 | 1 | 237 | 213 | 450 |
| | | | Total | 243 | 250 | 493 |

There are in addition five instances in which the sex of the captor is not recorded.

### 6. ANALYSIS OF THE RECORDS OF PREY.

As indicated in Table 2, the prey consists of 211 Orthoptera, 89 Hymenoptera, 74 Diptera, 56 Lepidoptera, 35 Hemiptera, 23 Coleoptera, 3 Neuroptera, 2 Mecoptera, 2 Odonata and 1 Isoptera. In two instances the prey is missing. The enormous preponderance of ORTHOPTERA is largely due to *Alcimus setifemoratus* which secured 53 per cent. of Orthoptera out of a total of 231 prey, and *Philodicus swynnertoni* for which the corresponding figures are 39 per cent. and 117. Strangely enough, there are only two Tettigonidae and one Gryllid as prey, the remainder being all Acridiidae. Since none of the Asilid captors is very small and most were captured in grassy situations or in coffee plantations where Acridiidae were very abundant, it might be expected that Orthoptera would form a considerable proportion of the prey. Many species of Asilidae sit about in exposed situations making "capture-darts" at passing insects; only certain groups attack resting insects. Insects which fly near or alight frequently on the ground are, therefore, very likely to be attacked; this is especially so in the case of grasshoppers which would be secured either when leaping or during longer flights; apterous individuals, which are well represented in the collection, would invariably be secured when leaping.

The HYMENOPTERA, with the exception of seven Ichneumonoidea, consist entirely of Aculeata. There are no ants as prey, but the capture of these insects is restricted to the limited period during which they possess wings and take to

flight. Bees are more than twice as numerous as the rest of the Hymenoptera together, but only about a quarter of them are the African wild form of *Apis mellifera*. The wasps include several large and powerful species.

Table 2. *Analytical table of the families of prey.*

23 Coleoptera
- 4 *Adephaga*
  - 4 Cicindelidae
- 1 *Diversicornia*
  - 1 Buprestidae
- 7 *Lamellicornia*
  - 7 Scarabaeidae
    - 1 Cetoniinae
    - 4 Copriinae
    - 2 Rutelinae
- 10 *Phytophaga*
  - 7 Cerambycidae
  - 3 Chrysomelidae
- 1 *Rhyncophora*
  - 1 Curculionidae

74 Diptera
- 48 Asilidae
- 19 Bombyliidae
- 6 Syrphidae
- 1 Tabanidae

35 Hemiptera
- 15 *Heteroptera*
  - 1 Coreidae
  - 8 Lygaeidae
  - 5 Pentatomidae
  - 1 Reduviidae
- 20 *Homoptera*
  - 19 Cicadidae
  - 1 Jassidae

89 Hymenoptera
- 62 *Apoidea*
  - 3 Andrenidae
  - 16 Apidae
  - 22 Anthophoridae
  - 20 Megachilidae
  - 1 Nomadidae
- 7 *Ichneumonoidea*
  - 2 Braconidae
  - 5 Ichneumonidae
- 6 *Sphecoidea*
  - 1 Bembecidae
  - 1 Larridae
  - 4 Sphecidae
- 14 *Vespoidea*
  - 2 Eumenidae
  - 1 Mutillidae
  - 3 Pompilidae
  - 7 Scoliidae
  - 1 Vespidae

1 Isoptera

56 Lepidoptera
- 6 *Noctuina*
  - 5 Noctuidae
  - 1 Syntomidae
- 4 *Notodontina*
  - 1 Bombycidae
  - 2 Geometridae
  - 1 Sphingidae

Lepidoptera (*cont.*)
- 43 *Papilionina*
  - 2 Hesperiidae
  - 12 Lycaenidae
  - 20 Nymphalidae
    - 8 Acraeinae
    - 7 Nymphalinae
    - 5 Satyrinae
  - 4 Papilionidae
  - 5 Pieridae
- 2 *Pyralidina*
  - 2 Pyralidae
- 1 *Tineina*
  - 1 Sesiidae

2 Mecoptera
- 2 Bittacidae

3 Neuroptera
- 1 Ascalaphidae
- 2 Chrysopidae

2 Odonata
- 2 Libellulidae

211 Orthoptera
- 208 Acrididae
- 1 Gryllidae
- 2 Tettigoniidae

2 Prey missing

498 Total

Table 3. *Analytical table of the numbers of prey recorded for each species.*

| | Coleoptera | Diptera | Hemiptera | Hymenoptera | Isoptera | Lepidoptera | Mecoptera | Neuroptera | Odonata | Orthoptera | Prey missing | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *M. ustulatum* Engel | 2 | 4 | 2 | 4 | . | . | . | . | . | 8 | . | 20 |
| *M. nigrostriatum* Hobby | 2 | 3 | 1 | . | . | . | . | . | . | 3 | . | 9 |
| *N. lugubris* Becker | 1 | . | . | 1 | . | . | 1 | . | . | . | . | 3 |
| *Neolaparus* sp. J. | . | . | . | . | . | 1 | . | . | . | . | . | 1 |
| *Neolaparus* sp. Q. | 1 | . | . | . | . | . | . | . | . | . | . | 1 |
| *L. albicincta* Loew. | . | 1 | . | 1 | . | . | . | . | . | 3 | . | 5 |
| *P. rufibarbis* Fab. | . | . | . | 3 | . | 1 | . | . | . | . | . | 4 |
| *P. aequalis* Loew. | 3 | 3 | 1 | 7 | . | . | . | . | . | 6 | . | 20 |
| *P.* sp. ? *robertii* Macq. | . | . | . | 1 | . | . | . | . | . | . | . | 1 |
| *P. swynnertoni* Hobby | 5 | 20 | 13 | 32 | . | 1 | 1 | . | . | 45 | . | 117 |
| *P. nigripes* Ricardo | 2 | 7 | 5 | 10 | . | 1 | . | . | . | 8 | . | 33 |
| *A. setifemoratus* Hobby | 5 | 25 | 9 | 11 | 1 | 52 | . | 3 | 2 | 122 | 1 | 231 |
| *N. rhodesiensis* Hobby | 2 | 8 | 2 | 17 | . | . | . | . | . | 9 | 1 | 39 |
| *M. nigroflavipes* Hobby | . | 2 | 2 | 2 | . | . | . | . | . | 6 | . | 12 |
| *S. aurulentus* Engel | . | . | . | . | . | . | . | . | . | 1 | . | 1 |
| Asilinae sp. indet. | . | 1 | . | . | . | . | . | . | . | . | . | 1 |
| Total | 23 | 74 | 35 | 89 | 1 | 56 | 2 | 3 | 2 | 211 | 2 | 498 |

DIPTERA are represented by only four families, the Asilidae (48 = 65 per cent.) and Bombyliidae (19 = 26 per cent.) predominating. This is partly due to the captors being better adapted for the capture of medium- and large-sized insects than for small ones; insects belonging to families composed entirely of smaller flies can, therefore, scarcely be expected as prey. Both the Asilidae and Bombyliidae are especially liable to be attacked because of the frequency with which they alight on the ground. The great preponderance of Asilidae is due to the selection of more or less open hunting-grounds by many species of Asilidae; suitable areas of such a nature are limited in number and are frequently occupied by several species. These Diptera, therefore, become fairly common in such areas and are likely to be caught by other Asilidae, either by their own kind or by different species.

The LEPIDOPTERA, all but four of which were caught by *Alcimus setifemoratus*, are mostly butterflies, but include also a few day-flying moths and others which probably fly readily when disturbed. The Nymphalidae and Lycaenidae predominate. The HEMIPTERA include 15 Heteroptera and 20 Homoptera; of these, nineteen are Cicadidae. COLEOPTERA, although not numerous, include representatives of six families. The Cicindelidae and Buprestidae are especially associated with clearings and are extremely active during the day. The Scarabaeidae are less active, but the subfamily Copriinae fly freely by day in search of dung.

The remaining orders are very poorly represented: The NEUROPTERA comprise two Chrysopidae and one Ascalaphid. The former are crepuscular or nocturnal and are not very active during the day; they are much more likely to be attacked by predacious insects such as Reduviidae, which creep about among vegetation, than by Asilidae. The Ascalaphidae are themselves actively predacious and might be expected as prey much more frequently than is actually the case. Two Libellulidae are the only examples of ODONATA as prey. A number of instances of attack against this order have been recorded by previous authors, but there is no reason to believe that Asilidae are ever important enemies of the group. In certain situations dragonflies and Asilidae occur together, but on the whole Asilidae frequent much drier habitats than do Odonata. Additional safeguard against attack is afforded by rapid flight several feet above the ground –a common habit of many of the larger dragonflies. Two MECOPTERA (Bittacidae) and a single *Isopteron* complete the list.

### 7. Rhodesian Asilidae as enemies of specially protected insects.

Among the COLEOPTERA recorded as prey, the Cicindelidae, Buprestidae, Scarabaeidae, Cerambycidae and Chrysomelidae are protected by their hardness, by secretions or both. The DIPTERA include only four families; of these, some Asilidae, Bombyliidae and Syrphidae may be said to be protected inasmuch as they enter into a mimetic association (probably Batesian) with

Hymenoptera. The HEMIPTERA-HETEROPTERA are notorious for their distasteful qualities, the HOMOPTERA are more or less procryptic, but are probably little attacked by Vertebrate enemies. HYMENOPTERA occur as prey of no less than 11 of the 16 species studied, but those Asilidae for which no Hymenopterous prey are recorded are represented by few individuals and the number of species attacking Hymenoptera is probably much greater. Altogether 89 Hymenoptera are contained in the collection, the majority of these are Aculeates protected by the possession of stings, but all are more or less protected by their tough integument and probably also by secretions. The LEPIDOPTERA include a Syntomid and eight Acraeas, all typical aposematic insects. There are also two Pierinae, two *Charaxes* and four Papilios which are usually considered to be protected. The NEUROPTERA include two Chrysopidae probably protected by odoriferous glands, although only certain species of the family have such organs well developed. The ORTHOPTERA consist largely of palatable procryptic species, but include some with brightly coloured hindwings which may be more or less distasteful, and a few typical aposematic species such as *Zonocerus elegans*.

The above list accounts for about a quarter of the total number of prey, but it is better not to treat this question statistically because of the lack of experimental data which would enable one to gauge the relative palatability of the actual species captured. It is certain, however, that the Rhodesian Asilidae frequently capture insects which are considered to be specially defended against the attacks of Vertebrates. This does not necessarily mean that these predators specially seek out such insects (although in some instances it may be so), nor that Asilidae are necessarily important enemies of them. It may, however, indicate a more tolerant sense of smell and taste than that possessed by Vertebrates, and, because of the manner in which the prey is caught, and the rapidity with which it is killed, a complete disregard for the stings of Aculeates.

## 8. Summary.

1. The collection was made in 1911 and 1912 by Mr C. F. M. Swynnerton in pasture land, coffee plantations, forest and forest outskirts at 3800–3900 ft. on Mount Chirinda, South-east Rhodesia; a description of the locality is given.

2. 498 individual insects are recorded as the prey of 16 species of Asilidae.

3. The structural adaptations of the Asilidae for the capture of prey are described, and considered in relation to the size and texture of the insects captured.

4. The preponderance of Orthopterous prey (211 specimens) is largely due to the records for *Alcimus setifemoratus* and *Philodicus swynnertoni*. It is most probably the result of local abundance, method of hunting and structural adaptation for the capture of large-sized insects rather than preferential selection. The Hymenoptera (89) consist chiefly of Aculeata. Diptera (74) are represented by only four families, the Asilidae and Bombyliidae predominating.

The Lepidoptera (56) are mostly butterflies. The Hemiptera (35) included nineteen Cicadidae and the Coleoptera (23) representatives of six families. The remaining orders are poorly represented (3 Neuroptera, 2 Mecoptera, 2 Odonata and 1 Isopteron).

5. The records suggest that *Alcimus setifemoratus* especially attacks Lepidoptera.

6. Many of the insects captured as prey are species considered to be specially defended against the attacks of Vertebrates.

7. Male and female captors occur in approximately equal numbers, but this is largely due to an excess of males in three species; apart from these the remaining species show the same predominance of females noted in previous investigations.

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## Table 4. *List of Asilidae and their prey.*

All captured by Mr C. F. M. Swynnerton at about 3800–3900 ft. on Mount Chirinda, South-eastern Rhodesia.

*Abbreviations used.* C.P. = coffee plantation; P. = pasture; F. = forest; C.O. = Chirinda outskirts.

First column: Serial number and sex of captor. Second column: Prey, sex and habitat. Third column: Date.

PREY OF *MICROSTYLUM USTULATUM* ENGEL.

| | | |
|---|---|---|
| | COLEOPTERA | |
| | Scarabaeidae | |
| 1. ♀ | *Clinteria infuscata* Gory and Perch, C.P. | 23. 12. 11 |
| 2. ♀ | *Popillia laetans* Perch, ♀, P. | 15. 1. 12 |
| | DIPTERA | |
| | Asilidae | |
| 3. ♀ | *Neolaparus* sp. E, ♀, P. | 14. 1. 12 |
| 4. ♀ | *N.* sp. G, ♂, P. | 20. 12. 11 |
| 5. ♀ | *N.* sp. I, ♂, C.P. | 23. 12. 11 |
| | Bombyliidae | |
| 6. ♀ | *Bombylius analis* Fab., ♀, P. | 26. 12. 11 |
| | HEMIPTERA | |
| | Cicadidae | |
| 7. ♂ | *Melampsalta* sp., ♂, P. | 21. 12. 11 |
| 8. ♀ | *M.* sp., ♂, P. | 5. 1. 12 |
| | HYMENOPTERA | |
| | Anthophoridae | |
| 9. ♀ | *Anthophora capensis* Friese, ♂, P. | 27. 12. 11 |
| 10. ♀ | do. ♂, P. | 4. 1. 12 |
| | Megachilidae | |
| 11. ♂ | *Megachile* sp. near *africana* Mocs., ♀, P. | 4. 1. 12 |
| | Scoliidae | |
| 12. ♀ | *Dielis collaris* Sichel, ♂, P. | 15. 1. 12 |
| | ORTHOPTERA | |
| | Acridiidae | |
| 13. ♀ | *Chrotogonus rotundatus* Kirby, ♀, P. | 15. 12. 11 |
| 14. ♀ | *Duronia chloronota* Stål, ♀, P. | 3. 1. 12 |
| 15. ♀ | Eumastacinae sp. indet., ♀, P. | 15. 12. 11 |
| 16. ♀ | *Gastrimargus africanus* Sauss., ♂, P. | 14. 12. 11 |
| 17. ♀ | *G.* sp., imm., ♀, P. | 3. 1. 12 |
| 18. ♀ | *Heteropternis saussurei* Kirby, ♀, P. | 21. 12. 11 |
| 19. ♀ | *Paracomacris productus* Walk., ♂, P. | 27. 12. 11 |
| 20. ♀ | Specimen untraced, P. | 4. 1. 12 |

PREY OF *MICROSTYLUM NIGROSTRIATUM* HOBBY.

| | | |
|---|---|---|
| | COLEOPTERA | |
| | Cerambycidae | |
| 1. ♀ | *Dirphya leucostigma* Harold, ♂, P. | 24. 12. 11 |
| 2. ♀ | *D. trigonifera* Auriv., ♀, P. | 28. 12. 11 |
| | DIPTERA | |
| | Asilidae | |
| 3. ♀ | *Neolaparus* sp. C, ♀, P. | 14. 1. 12 |
| 4. ♀ | *N.* sp. Q, ♀, P | 22. 12. 11 |
| | Bombyliidae | |
| 5. ♂ | *Geron gibbosus* Meig., ♂, P. | 14. 12. 11 |
| | HEMIPTERA | |
| | Cicadidae | |
| 6. ♀ | *Melampsalta* sp., ♂, P. | 14. 12. 11 |
| | ORTHOPTERA | |
| | Acridiidae | |
| 7. ♀ | *Aulacobothrus* sp., ♀, P. | 14. 12. 11 |
| 8. ♀ | *Duronia* sp. imm., ♀, P. | 19. 12. 11 |
| 9 ♀ | *Paracomacris productus* Walk., ♂, P. | 3. 1. 12 |

PREY OF *NEOLAPARUS LUGUBRIS* BECKER.

| | | |
|---|---|---|
| | COLEOPTERA | |
| | Galerucidae | |
| 1. ♀ | ? *Monolepta* sp., ♂ | 3. 1. 12 |
| | HYMENOPTERA | |
| | Vespidae | |
| 2. ♀ | *Icaria distigma* Gerst., ♀ | 28. 12. 11 |
| | MECOPTERA | |
| | Bittacidae | |
| 3. ♀ | *Bittacus montanus* Weele, ♀, P. | 11. 1. 12 |

PREY OF *NEOLAPARUS* SP. J.

| | | |
|---|---|---|
| | LEPIDOPTERA | |
| | Syntomidae | |
| 1. ♀ | *Euchromia amoena* Moeschl., ♀, C.P. | 19. 12. 11 |

Table 4 (*cont.*).

| | | |
|---|---|---|
| | PREY OF *NEOLAPARUS* SP. Q. | |
| | COLEOPTERA | |
| | Chrysomelidae | |
| 1. ♀ | ? Galerucinae sp. indet. | 3. 1. 12 |
| | PREY OF *LAXENECERA ALBICINCTA* LOEW. | |
| | DIPTERA | |
| | Bombyliidae | |
| 1. ♀ | *Exoprosopa balioptera* Loew. ? ♂, P. | 16. 2. 12 |
| | HYMENOPTERA | |
| | Ichneumonidae | |
| 2. ♀ | Genus near *Catoglyptus* Holmg., ♀, P. | 5–20. 3. 12 |
| | ORTHOPTERA | |
| | Acridiidae | |
| 3. ♂ | *Acrotylus patruelis* H.-Sch., imm., ♀, P. | 5–20. 3. 12 |
| 4. ♂ | *Gymnobothrus linea-alba* Bol., ♂, P. | 9. 2. 12 |
| 5. ♀ | do. ♀, P. | 25. 2. 12 |
| | PREY OF *PROAGONISTES RUFIBARBIS* FAB. | |
| | HYMENOPTERA | |
| | Anthophoridae | |
| 1. ♀ | *Anthophora capensis* Friese, ♀, C.P. | 21. 12. 11 |
| | Larridae | |
| 2. ♀ | *Notogonia* sp., ♀ | 28. 12. 11 |
| | Sphecidae | |
| 3. ♀ | *Ammophila capensis* Lep., ♀ | 28. 12. 11 |
| | LEPIDOPTERA | |
| | Noctuidae | |
| 4. ♂ | Agrotinae, sp. indet., ♂, C.P. | 23. 12. 11 |
| | PREY OF *PROMACHUS AEQUALIS* LOEW. | |
| | COLEOPTERA | |
| | Chrysomelidae | |
| 1. ♀ | *Antipus rufus* De G., ?, P. | 5–20. 3. 12 |
| | Cicindelidae | |
| 2. ♂ | *Cicindela disjuncta* Dej., ♀, C.P. | 21. 12. 11 |
| | Scarabaeidae | |
| 3. ♀ | *Popillia laetans* Perch, ♂, P. | 16. 2. 12 |
| | DIPTERA | |
| | Asilidae | |
| 4. ♂ | *Neolaparus* sp. G, ♀, P. | 5. 1. 12 |
| | Bombyliidae | |
| 5. ♀ | *Bombylius analis* Fab., ♀, P. | 9. 2. 12 |
| | Syrphidae | |
| 6. ♀ | *Eristalis* sp. ? *taeniops* Wied., ♀, P. | 9. 2. 12 |
| | HEMIPTERA | |
| | Lygaeidae | |
| 7. ♀ | *Lygaeus rivularis* Germ., ♀, P. | 28. 2. 12 |
| | HYMENOPTERA | |
| | Anthophoridae | |
| 8. ♂ | *Anthophora capensis* Friese, ♂, P. | 5–20. 3. 12 |
| 9. ♀ | do. ♂, P. | 28. 2. 12 |
| | Ichneumonidae | |
| 10. ♂ | *Hemipimpla vipioides* Brullé, ♀, P. | 5–20. 3. 12 |
| 11. ♀ | *Ischnojoppa luteator* Fab., var. *unicolor* Monl., ♂, P. | 6. 1. 12 |
| | Megachilidae | |
| 12. ♂ | *Megachile nasalis* Smith, ♀, P. | 5–20. 3. 12 |
| | Nomadidae | |
| 13. ♀ | *Crocisa calceata* Vachal, ♀, P. | 5–20. 3. 12 |
| | Sphecidae | |
| 14. ♀ | *Sphex marginatus* Smith, ♀, P. | 5–20. 3. 12 |
| | ORTHOPTERA | |
| | Acridiidae | |
| 15. ♂ | *Heteropternis saussurei* Kirby, ♂, P. | 28. 2. 12 |
| 16. ♀ | *Orthochtha bisulcata* Krauss, ♂, P. | 5–20. 3. 12 |
| 17. ♀ | *Paracomacris productus* Walk., ♀, P. | 5–20. 3. 12 |
| 18. ♀ | *Pseudochrista temporalis* Stål, ♂ | 28. 2. 12 |
| 19. ♂ | *Ticra pictipes* Bol., ♂, P. | 13. 1. 12 |
| 20. ♂ | *Trilophidia angustipennis* Kirby, ♂, P. | 28. 2. 12 |

Table 4 (*cont.*).

PREY OF *PROMACHUS* SP.? *ROBERTII* MACQ.

| | | | |
|---|---|---|---|
| | HYMENOPTERA | | |
| | Eumenidae | | |
| 1. ♀ | *Odynerus* sp., ♂, C.O. | | 3. 1. 12 |

PREY OF *PHILODICUS SWYNNERTONI* HOBBY.

| | | | |
|---|---|---|---|
| | COLEOPTERA | | |
| | Curculionidae | | |
| 1. ♂ | *Phacemastix poultoni* Mshl., ♀, P. | | 29. 1. 12 |
| | Cerambycidae | | |
| 2. ♂ | *Dirphya leucostigma* Harold, ♀, P. | | 16. 1. 12 |
| 3. ♂ | do. | ♀, P. | 7. 2. 12 |
| 4. ♀ | do. | ♀, P. | 19. 1. 12 |
| 5. ♀ | do. | ♀, P. | 2. 2. 12 |
| | DIPTERA | | |
| | Asilidae | | |
| 6. ♀ | *Hoplistomera serripes* Fáb., ♂, P. | | 17. 2. 12 |
| 7. ♂ | *Laxenecera albicincta* Loew, ♀, P. | | 17. 2. 12 |
| 8. ♂ | *Neolaparus* sp. A, ♂, P. | | 27. 1. 12 |
| 9. ♂ | *N.* sp. E, ♀, P. | | 27. 1. 12 |
| 10. ♀ | do. | ♀, P. | 25. 1. 12 |
| 11. ♀ | do. | ♀, P. | 28. 1. 12 |
| 12. ♂ | *N.* sp. G, ♀, P. | | 16. 1. 12 |
| 13. ♂ | do. | ♀, P. | 19. 1. 12 |
| 14. ♀ | do. | ♂, P. | 11. 1. 12 |
| 15. ♀ | do. | ♂, P. | 1. 2. 12 |
| | Bombyliidae | | |
| 16. ♂ | *Bombylius analis* Fab., ♂, P. | | 12–13. 2. 12 |
| 17. ♂ | do. | ♀, P. | 5–20. 3. 12 |
| 18. ♀ | do. | ♂, P. | 12. 1. 12 |
| 19. ♀ | do. | ♀, P. | 24. 1. 12 |
| 20. ♀ | do. | ♀, P. | 20. 2. 12 |
| 21. ♀ | do. | ♀, P. | 21. 2. 12 |
| 22. ♂ | *Systoechus* sp., ♀, P. | | 8. 2. 12 |
| | Syrphidae | | |
| 23. ♂ | *Eristalis* sp. ? *taeniops* Wied., ♀, P. | | 14. 2. 12 |
| 24. ♂ | *Senaspis elliotii* Aust., ♀ | | 12 13. 2. 12 |
| | Tabanidae | | |
| 25. ♂ | *Rhinomyza denticornis* Wied., ♀, P. | | 14. 2. 12 |
| | HEMIPTERA | | |
| | Cicadidae | | |
| 26. ♂ | *Melampsalta* sp., ♂, P. | | 19. 1. 12 |
| 27. ♂ | do. | ♂, P | 5. 2. 12 |
| 28. ♂ | do. | ♂, P | 14. 2. 12 |
| 29. ♀ | do. | ♂, P | 13. 1. 12 |
| 30. ♀ | do. | ♂, P. | 19. 1. 12 |
| 31. ♀ | do. | ♂, P. | 29. 1. 12 |
| 32. ♀ | do. | ♂, P. | 12–13. 2. 12 |
| | Lygaeidae | | |
| 33. ♂ | *Lygaeus rivularis* Germ., ♀, P. | | 16. 1. 12 |
| 34. ♂ | do. | ♀, P. | 5. 2. 12 |
| 35. ♂ | do. | ♀, P. | 5. 2. 12 |
| 36. ♀ | do. | ♀, P. | 2. 2. 12 |
| | Pentatomidae | | |
| 37. ♀ | ? *Diploxys rostrata* Fab., ? ♂, P. | | 6. 1. 12 |
| | Reduviidae | | |
| 38. ♂ | Specimen untraced, P. | | 7. 2. 12 |
| | HYMENOPTERA | | |
| | Andrenidae | | |
| 39. ♀ | *Nomia vulpina* Gerst., ♀, P. | | 21. 2. 12 |
| | Anthophoridae | | |
| 40. ♀ | *Anthophora acraensis* Fab., var. *albocaudata* Dours., ♀, P. | | 7. 2. 12 |
| 41. ♂ | *A. africana* Friese, ♀, P. | | 25. 1. 12 |
| 42. ♂ | *A. albigena fallax* Smith, ♀, P. | | 6. 1. 12 |
| 43. ♀ | do. | ♀, P. | 23. 12. 11 |
| 44. ♀ | *A. capensis* Friese, ♀, P. | | 24. 1. 12 |
| 45. ♀ | do. | ♀, P. | 6. 2. 12 |
| 46. ♀ | do. | ♀, P. | 16. 2. 12 |
| 47. ♀ | do. | ♀, P. | 18. 2. 12 |
| 48. ♂ | *A. torrida* Smith, ♀, P. | | 5–20. 3. 12 |
| | Apidae | | |
| 49. ♂ | *Apis mellifera unicolor* Latr. var. *adansoni* Latr., ☿, P. | | 31. 1. 12 |
| 50. ♂ | do. | ☿, P. | 4. 2. 12 |
| 51. ♂ | do. | ☿, P. | 8. 2. 12 |
| 52. ♂ | do. | ☿, P. | 12–13. 2. 12 |

Table 4 (*cont.*).

| | | |
|---|---|---|
| | HYMENOPTERA (*cont.*) | |
| | Bombyliidae | |
| 53. ♂ | *Bombyx capensis* Lep., ♀, P. | 15. 2. 12 |
| | Braconidae | |
| 54. ♂ | *Iphiaulax* sp., ♀, P. | 26. 1. 12 |
| | Ichneumonidae | |
| 55. ♂ | *Echthromorpha* sp., ♀, P. | 28. 1. 12 |
| 56. ♀ | *Hemipimpla vipioides* Brullé, ♀, P. | 15. 2. 12 |
| | Megachilidae | |
| 57. ♀ | *Megachile nasalis* Smith, ♀, P. | 28. 1. 12 |
| 58. ♂ | do. ♀, P. | 12 13. 2. 12 |
| 59. ♂ | *M. temora* Cam., ♀, P. | 31. 1. 12 |
| 60. ♂ | *M.* sp. ♂, P. | 4. 2. 12 |
| 61. ♂ | do. ♀, P. | 14. 2. 14 |
| 62. ♂ | do. ♀, P. | 5-20. 3. 12 |
| 63. ♀ | *Serapis denticulata* Smith, ♀, P. | 25. 1. 12 |
| | Mutillidae | |
| 64. ♀ | *Mutilla purpurata* Smith, ♂, P. | 27. 1. 12 |
| | Scoliidae | |
| 65. ♂ | *Dielis mansueta* Gerst., ♂, P. | 14. 1. 12 |
| 66. ♂ | do. ♂, P. | 24. 1. 12 |
| 67. ♂ | do. ♂, P. | 12. 1. 12 |
| 68. ♀ | do. ♂, P. | 13. 1. 12 |
| 69. ♀ | do. ♂, P. | 2. 2. 12 |
| | Sphecidae | |
| 70. ♀ | *Tachytes mira* Kohl, ♀, P. | 6. 1. 12 |
| | LEPIDOPTERA | |
| | Sesiidae | |
| 71. ♀ | *Chamaesphecia ethiopica* Hmpsn., ♂, P. | 31. 1. 12 |
| | MECOPTERA | |
| | Bittacidae | |
| 72. ♂ | *Bittacus montanus* Weele, ♀, P. | 11. 1. 12 |

| | | |
|---|---|---|
| | ORTHOPTERA | |
| | Acridiidae | |
| 73. ♂♀ | *Duronia chloronota* Stal. ♂, P. | 16. 1. 12 |
| 74. ♂♀ | do. ♂, P. | 1. 2. 12 |
| 75. ♂♀ | do. ♂, P. | 6. 2. 12 |
| 76. ♂♀ | do. ♂, P. | 12–13. 2. 12 |
| 77. ♂ | *Eucoptacra* sp., ♂, P. | 5. 2. 12 |
| 78. ♂ | *Gymnobothrus linea-alba* Bol., ♂, P. | 24. 1. 12 |
| 79. ♂ | do. ♂, P. | 31. 1. 12 |
| 80. ♂ | do. ♂, P. | 1. 2. 12 |
| 81. ♂♂ | do. ♂, P. | 2. 2. 12 |
| 82. ♂ | do. ♂, P. | 11. 2. 12 |
| 83. ♂ | do. ♂, P. | 5–20. 3. 12 |
| 84. ♂♀ | do. ♂, P. | 6. 1. 12 |
| 85. ♂ | do. ♂, P. | 11. 1. 12 |
| 86. ♂ | do. ♂, P. | 14. 1. 12 |
| 87. ♂♀ | do. ♂, P. | 4. 2. 12 |
| 88. ♂ | do. ♂, P. | 5. 2. 12 |
| 89. ♂♀ | do. ♂, P. | 12–13. 2. 12 |
| 90. ♂♀ | do. ♂, P. | 15. 2. 12 |
| 91. ♂ | do. ♂, P. | 17. 2. 12 |
| 92. ♂ | *Heteropternis saussurei* Kirby, ♂, P. | 29. 1. 12 |
| 93. ♂ | *H. couloniana* Sauss., ♂, P. | 1. 2. 12 |
| 94. ♂ | *Lentula* sp. ? *candidoi* Ramme, ♂, P. | 26. 1. 12 |
| 95. ♂ | *Orthochtha bisulcata* Krauss, ♂, P. | 22. 2. 12 |
| 96. ♂ | do. ♂, P. | 31. 1. 12 |
| 97. ♂ | do. ♂, P. | 7. 2. 12 |
| 98. ♀ | do. ♂, P. | 8. 2. 12 |
| 99. ♂ | *Paracomacris productus* Walk., ♂, P. | 27. 1. 12 |
| 100. ♂ | do. ♂, P. | 28. 1. 12 |
| 101. ♂ | do. ♂, P. | 5. 2. 12 |
| 102. ♂ | do. ♂, P. | 6. 2. 12 |
| 103. ♂ | do. ♂, P. | 14. 2. 12 |
| 104. ♂ | do. ♂, P. | 29. 1. 12 |
| 105. ♂ | do. ♂, P. | 6. 2. 12 |
| 106. ♂ | do. ♂, P. | 14. 2. 12 |
| 107. ♂ | do. ♂, P. | 22. 2. 12 |
| 108. ♂ | do. ♂, P. | 22. 2. 12 |
| 109. ♂ | *Pseudochirista temporalis* Stål, ♂, P. | 26. 1. 12 |
| 110. ♂ | do. ♂, P. | 4. 2. 12 |
| 111. ♂ | do. ♂, P. | 8. 2. 12 |

Table 4 (*cont.*).

| | | |
|---|---|---|
| | Orthoptera Acridiidae (*cont.*) | |
| 112. ♂ | *Pseudochirista temporalis* Stål, ♀, P. | 12–13. 2. 12 |
| 113. ♀ | do. ♀, P. | 26. 1. 12 |
| 114. ♀ | do. ♀, P. | 2. 12 |
| 115. ♂ | Tetriginae sp. indet., P. | 11. 2. 12 |
| 116. ♂ | *Trilophidia angustipennis* Kirby, ♂, P. | 4. 2. 12 |
| 117. ♂ | *Tristria* sp., ♂, P. | 24. 1. 12 |
| | PREY OF *PHILODICUS NIGRIPES* RICARDO. | |
| | Coleoptera | |
| | Buprestidae | |
| 1. ♀ | ? *Discoderes* sp., P. | 13. 1. 12 |
| | Cerambycidae | |
| 2. ♂ | *Dirphya leucostigma* Harold, ♀, P. | 5–20. 3. 12 |
| | Diptera | |
| | Asilidae | |
| 3. ♂ | *Laxenecera* sp., ♂, P. | 19. 2. 12 |
| 4. ♂ | *Neolaparus* sp. B, ♀, P. | 4. 1. 12 |
| 5. ♂ | *N.* sp. C, ♀, P. | 14. 12. 11 |
| 6. ♂ | *N.* sp. E, ♀, P. | 23. 12. 11 |
| 7. ♂ | *N.* sp. P, ♂, P. | 17. 12. 11 |
| | Syrphidae. | |
| 8. ♀ | *Syrphus* sp. ? *aegyptius* Wied., ♂, P. | 5–20. 3. 12 |
| 9. ♂ | *S.* sp., ♀, P. | 19. 2. 12 |
| | Hemiptera | |
| | Cicadidae | |
| 10. ♂ | *Melampsalta* sp., ♂, P. | 4. 1. 12 |
| 11. ♀ | *M.* sp., ♀, P. | 13. 1. 12 |
| 12. ♀ | *M.* sp., ♂, P. | 6. 2. 12 |
| | Lygaeidae | |
| 13. ♀ | *Lygaeus rivularis* Germ., ♀, P. | 2. 2. 12 |
| | Pentatomidae | |
| 14. ♀ | Larva sp. indet., P. | 4. 3. 12 |
| | Hymenoptera | |
| | Andrenidae | |
| 15. ♀ | *Nomia fulvohirta* Smith, ♀, P. | 19. 2. 12 |
| 16. ♀ | *N.* sp., ♂, P. | 26. 12. 11 |
| | Anthophoridae | |
| 17. ♀ | *Anthophora albigena fallax* Smith, ♀, P. | 4. 1. 12 |
| 18. ♀ | *A. capensis* Friese, ♀, P. | 5–20. 3. 12 |
| 19. ♀ | *A. torrida* Smith, ♀, P. | 5 20. 3. 12 |
| | Apidae | |
| 20. ♂ | *Apis mellifera unicolor* Latr., var. *adansoni* Latr., ♀, P. | 18. 2. 12 |
| 21. ♀ | do. ♀, P. | 18. 2. 12 |
| | Eumenidae | |
| 22. ♀ | *Odynerus* sp. near *quadrituberculatus* Smith, ♀, P. | 16. 2. 12 |
| | Megachilidae | |
| 23. ♀ | *Megachile funebris* Rad., ♀, P. | 5–20. 3. 12 |
| 24. ♀ | *M. gratiosa* Gerst., ♂, P. | 19. 2. 12 |
| | Lepidoptera | |
| | Noctuidae | |
| 25. ♀ | *Laphygma exempta* Walk., ♀, P. | 16. 2. 12 |
| | Orthoptera | |
| | Acridiidae | |
| 26. ♀ | *Chirindites marshalli* Ramme, ♀, P. | 24. 12. 11 |
| 27. ♂ | ? *Duronia* sp., immature, ♀, P. | 17. 12. 11 |
| 28. ♂ | *Gymnobothrus linea-alba* Bol., ♂, P. | 5-20. 3. 12 |
| 29. ♀ | do. ♂, P. | 18. 2. 12 |
| 30. ♂ | *Paracomacris productus* Walk., ♀, P. | 4. 3. 12 |
| 31. ♀ | do. ♂, P. | 4. 3. 12 |
| 32. ♀ | do. ♂, P. | 5–20. 3. 12 |
| 33. ♀ | Tryxalinae sp. indet., imm., ♀, P. | 17. 12. 11 |

Table 4 (*cont.*).

PREY OF *ALCIMUS SETIFEMORATUS* HOBBY.

| | | |
|---|---|---|
| | COLEOPTERA | |
| | Cicindelidae | |
| 1. ♂ | *Cicindela bertolinii* Horn, ♀, C.P. | 12. 12. 11 |
| 2. ♂ | do. ♀, C.P. | 23. 12. 11 |
| 3. ♀ | do. ♂, C.P. | 22. 12. 11 |
| | Scarabacidae | |
| 4. ♀ | *Onthophagus brucei* Reiche, ♀, P. | 25. 12. 11 |
| 5. ♂ | *O. panoplus* Bates, ♂, P. | 23. 12. 11 |
| | DIPTERA | |
| | Asilidae | |
| 6. ♀ | *Alcimus setifemoratus* Hobby, ♂, F. | 15. 12. 11 |
| 7. ♂ | *Hoplistomera serripes* Fab., ♀, P. | 15. 1. 12 |
| 8. ♂ | *Neolaparus* sp. C, ♂, P. | 16. 12. 11 |
| 9. ♂ | do. ♂, P. | 15. 1. 12 |
| 10. ♂ | *N.* sp. D, ♂, C.P. | 22. 12. 11 |
| 11. ♀ | do. ♂, C.P. | 20. 12. 11 |
| 12. ♀ | do. ♀, P. | 24. 12. 11 |
| 13. ♀ | do. ♂, P. | 28. 12. 11 |
| 14. ♂ | *N.* sp. E, ♂, C.P. | 23. 12. 11 |
| 15. ♂ | do. ♀, C.P. | 23. 12. 11 |
| 16. ♀ | do. ♂, C.P. | 22. 12. 11 |
| 17. ♀ | do. ♀, P. | 24. 12. 11 |
| 18. ♀ | do. ♀, P. | 26. 12. 11 |
| 19. ♂ | *N.* sp. F, ♀, C.P. | 21. 12. 11 |
| 20. ♂ | *N.* sp. G, ♂, F. | 26. 12. 11 |
| 21. ♂ | do. ♀, P. | 12. 1. 12 |
| 22. ♀ | do. ♂, C.P. | 19. 12. 11 |
| 23. ♀ | do. ♀, C.P. | 22. 12. 11 |
| 24. ♀ | *N.* sp. H, ♂, C.P. | 20. 12. 11 |
| 25. ♂ | *Promachus aequalis* Loew, ♀, C.P. | 23. 12. 11 |
| 26. ♂ | do. ♂ | 28. 12. 11 |
| 27. ♂ | *P.* sp. ? *robertii* Macq., ♀ | 3. 1. 12 |
| 28. ♀ | *Synolcus aurulentus* Engel, ♀, P | 14. 12. 11 |
| | Bombyliidae | |
| 29. ♂ | *Exoprosopa* sp. ? *balioptera* Loew, ♀, C.P. | 23. 12. 11 |
| 30. ♂ | *Lomatia pictipennis* Wied., P. | 25. 12. 11 |
| | HEMIPTERA | |
| | Cicadidae | |
| 31. ♂ | *Melampsalta* sp., ♂, P. | 16. 12. 11 |
| 32. ♀ | *M.* sp., ♀, C.P. | 23. 12. 11 |
| 33. ♂ | *Stagira* sp., ♂, C.P. | 21. 12. 11 |
| 34. ♂ | *S.* sp., ♂, C.P. | 21. 12. 11 |
| 35. ♂ | *S.* sp., ♂, C.P. | 22. 12. 11 |
| | Jassidae | |
| 36. ♂ | *Petalocephala* sp., ♀, P. | 15. 12. 11 |
| | Pentatomidae | |
| 37. ♂ | *Agonoscelis versicolor* Fab., ♂, P. | 13. 12. 11 |
| 38. ♀ | do. ♂, P. | 12. 1. 11 |
| 39. ♂ | Larva sp. indet., C.P. | 25. 12. 11 |
| | HYMENOPTERA | |
| | Anthophoridae | |
| 40. ♂ | *Anthophora africana* Friese, ♀, P. | 3. 1. 12 |
| 41. ♀ | *A. torrida* Smith, ♀, P. | 26. 12. 11 |
| | Apidae | |
| 42. ♂ | *Apis mellifera unicolor* Latr., var. *adansoni* Latr., ☿, C.P. | 21. 12. 11 |
| 43. ♂ | do. ☿, P. | 24. 12. 11 |
| 44. ♂ | do. ☿ | 3. 1. 12 |
| 45. ♀ | do. ☿, C.P. | 22. 12. 11 |
| 45. ♀ | do. ☿, C.P. | 23. 12. 11 |
| | Megachilidae | |
| 47. ♂ | *Megachile bituberculata* Rits., P. | 17. 12. 11 |
| 48. ♀ | *M.* sp. ? *ungulata* Smith, ♂, P. | 3. 1. 12 |
| | Scoliidae | |
| 49. ♀ | *Dielis mansueta* Gerst., ♂, P. | 26. 12. 11 |
| | Sphecidae | |
| 50. ♀ | *Ammophila capensis* Lep., ♀, C.P. | 22. 12. 11 |
| | ISOPTERA | |
| 51. ☽ | Sp. indet., P. | 18. 12. 11 |

Table 4 (*cont.*).

| | | |
|---|---|---|
| | Lepidoptera | |
| | Bombycidae | |
| 52. ♂ | *Olapa furva* Hmpsn., ♀, C.P. | 26. 12. 11 |
| | Geometridae | |
| 53. ♂ | *Leptaroa fulvicolora* Hmpsn., ♂ | 3. 1. 12 |
| 54. ♀ | *Nassunia caffraria* Linn., ♂, C.P. | 12. 12. 11 |
| | Hesperiidae | |
| 55. ♂ | *Caprona canopus* Trim., ♀ | 27. 12. 11 |
| 56. ♂ | *Kedestes capenas* Hew., ♂, C.P. | 12. 12. 11 |
| | Lycaenidae | |
| 57. ♂ | *Catochrysops malathana* Boisd., ♀, P. | 14. 12. 11 |
| 58. ♂ | do. ♂, C.P. | 16. 12. 11 |
| 59. ♀ | do. ♀, P. | 13. 12. 11 |
| 60. ♀ | do. ♂, P. | 14. 12. 11 |
| 61. ♀ | *Cacyreus lingeus* Cram., ♂ | 28. 12. 11 |
| 62. ♂ | *Polyommatus boeticus* Linn., ♀, C.P. | 26. 12. 11 |
| 63. ♂ | *Tarucus telicanus* Lang, ♀, C.P. | 12. 12. 11 |
| 64. ♂ | do. ♀, C.P. | 12. 12. 11 |
| 65. ♂ | do. ♂, C.P. | 13. 12. 11 |
| 66. ♂ | do. ♂, C.P. | 13. 12. 11 |
| 67. ♂ | do. ♀, C.P. | 13. 12. 11 |
| 68. ♂ | do. ♂, C.P. | 22. 12. 11 |
| | Noctuidae | |
| 69. ♂ | *Amyna punctum* Fab., ♀, C.P. | 16. 12. 11 |
| 70. ♀ | *Cerocala contraria* Walk., ♀, P. | 14. 12. 11 |
| 71. ♀ | *Euxoa* sp. ? *longidentifera* Hmpsn., or *segetum* Schiff., ♂, C.P. | 23. 12. 11 |
| | Nymphalidae | |
| 72. ♂ | *Acraea caldarena* Hew., ♀, C.P. | 12. 12. 11 |
| 73. ♂ | do. ♀, C.P. | 13. 12. 11 |
| 74. ♂ | do. ♂ | 28. 12. 11 |
| 75. ♀ | do. ♀ | 28. 12. 11 |
| 76. ♀ | *A. igola* Trim., ♂, C.P. | 12. 12. 11 |
| 77. ♂ | *A. neobule* Dbl., ♂, C.P. | 23. 12. 11 |
| 78. ♂ | *A. terpsichore* Linn., ♂, C.P. | 13. 12. 11 |
| 79. ♂ | do. ♀, C.P. | 13. 12. 11 |
| 80. ♂ | *Charaxes saturnus* Butl., ♀, P. | 14. 12. 11 |
| 81. ♂ | *C. zoolina* Westw., f. *neanthes* Hew., ♂, C.P. | 23. 12. 11 |
| 82. ♂ | *Crenis boisduvali* Walton, ♂, C.P. | 12. 12. 11 |
| 83. ♂ | do. ♂, C.P. | 12. 12. 11 |
| 84. ♀ | do. ♂, C.P. | 20. 12. 11 |
| 85. ♂ | *Lachnoptera ayresi* Trim., ♀, C.P. | 13. 12. 11 |
| 86. ♂ | *Mycalesis campina* Auriv., ♂, C.P. | 12. 12. 11 |
| 87. ♂ | do. ♂, C.P. | 23. 12. 11 |
| 88. ♀ | do. ♂, C.P. | 22. 12. 11 |
| 89. ♀ | do. ♂, P. | 4. 3. 12 |
| 90. ♂ | *M. safitza* Hew., ♀, C.P. | 26. 12. 11 |
| 91. ♂ | *Neptis swynnertoni* Trim., ♀, C.P. | 20. 12. 11 |
| | Papilionidae | |
| 92. – | *Papilio echerioides* Trim., ♀, C.P. | 25. 12. 11 |
| 93.* | *P. nireus lyaeus* Dbl., ♂ | |
| 94.* | *P. policenes* Cram., ♂ | 20. 12. 11 |
| 95. ♂ | *P. pylades angolanus* Goeze, ♀ | 26. 12. 11 |
| | Pieridae | |
| 96. ♂ | *Catopsilia florella* Fab., ♂, C.P. | 20. 12. 11 |
| 97. ♂ | *Leptosia alcesta* Cram., f. *medusa* Cram., ♂, C.P. | 19. 12. 11 |
| 98. ♂ | *Terias senegalensis* Boisd., ♂, C.P. | 20. 12. 11 |
| 99. ♂ | do. ♀, C.P. | 21. 12. 11 |
| 100.* | do. ♀ | 12. 12. 11 |
| | Pyralidae | |
| 101. ♂ | *Glyphodes elealis* Walk., ♂ | 27. 12. 11 |
| 102. ♂ | *Leucinodes orbonalis* Guen., ♂ | 27. 12. 11 |
| | Sphingidae | |
| 103. ♀ | *Macroglossa trochilus trochilus* Hübn., ♂, C.P. | 12. 12. 11 |
| | Neuroptera | |
| | Ascalaphidae | |
| 104. ♂ | *Encyoposis flavilinea* Walk., ♀, P. | 19. 12. 11 |
| | Chrysopidae | |
| 105. ♂ | *Chrysopa* sp. ? *umbrosa* Navás, C.P. | 23. 12. 11 |
| 106. ♀ | do. C.P. | 21. 12. 11 |

* Found dead in a locality frequented by Asilidae.

Table 4 (*cont.*).

| | | |
|---|---|---|
| | ODONATA | |
| | Libellulidae | |
| 107. ♂ | *Crocothemis sanguinolenta* Burm., ♂, C.P. | 23. 12. 11 |
| 108. ♀ | *Orthetrum stemmale capense* Calv., ♀, C.P. | 20. 12. 11 |
| | ORTHOPTERA | |
| | Acrididae | |
| 109. ♀ | *Acrotylus patruelis* H.-Sch., ♀, C.P. | 21. 12. 11 |
| 110. ♂ | do. ♀, C.P. | 23. 12. 11 |
| 111. ♀ | *Apnorisa fungosa* Bol., ♀, C.P. | 21. 12. 11 |
| 112. ♀ | *Aulacobothrus gracilus* Uvar., ♀, P. | 14. 12. 11 |
| 113. ♂ | *Cataloipus roscipennis* Uvar., ♂, P. | 29. 12. 11 |
| 114. ♂ | *Catantops maculatus* Karny, ♂, C.P. | 26. 12. 11 |
| 115. ♀ | *C. sulphureus* Walk., ♂, P. | 15. 12. 11 |
| 116. ♂ | Catantopinae sp. indet. imm., ♂, C.P. | 12. 12. 11 |
| 117. ♂ | do. ♀, C.P. | 12. 12. 11 |
| 118. ♂ | do. ♂, C.P. | 13. 12. 11 |
| 119. ♂ | do. ♀, C.P. | 13. 12. 11 |
| 120. ♂ | do. ♂, P. | 14. 12. 11 |
| 121. ♀ | do. ♂, C.P. | 22. 12. 11 |
| 122. ♂ | *Chirindites marshalli* Ramme, ♂, C.P. | 21. 12. 11 |
| 123. ♂ | *Chrotogonus hemipterus* Schaum, ♂, C.P. | 16. 12. 11 |
| 124. ♂ | *C. rotundatus* Kirby, ♀, C.P. | 12. 12. 11 |
| 125. ♂ | do. ♂, C.P. | 22. 12. 11 |
| 126. ♀ | do. ♀, C.P. | 21. 12. 11 |
| 127. ♂ | *Duronia chloronota* Stål, ♂, P. | 20. 12. 11 |
| 128. ♂ | do. ♂, P. | 21. 12. 11 |
| 129. ♀ | do. ♀, P. | 19. 12. 11 |
| 130. ♀ | do. ♂, P. | 20. 12. 11 |
| 131. ♀ | do. ♂, P. | 20. 12. 11 |
| 132. ♂ | *D.* sp. imm., ♂, P. | 13. 12. 11 |
| 133. ♂ | do. ♀, P. | 14. 12. 11 |
| 134. ♂ | do. ♀, P. | 14. 12. 11 |
| 135. ♂ | ? *D.* sp. imm., ♀, P. | 14. 12. 11 |
| 136. ♂ | *D.* sp. imm., ♀, P. | 14. 12. 11 |
| 137. ♂ | do. ♀, P. | 14. 12. 11 |
| 138. ♀ | do. ♂, P. | 14. 12. 11 |
| 139. ♀ | do. ♂, C.P. | 22. 12. 11 |
| 140. ♀ | do. ♀, P. | 29. 12. 11 |
| 141. ♀ | *Eucoptera* sp., ♀, P. | 29. 12. 11 |
| 142. ♂ | *Eupropacris ornatus* Karny, ♂, C.P. | 12. 12. 11 |
| 143. ♂ | Eumastacinae sp. indet., ♀, P. | 27. 12. 11 |
| 144. ♂ | do. ♂, C.P. | 20. 12. 11 |
| 145. ♂ | do. ♂, C.P. | 20. 12. 11 |
| 146. ♀ | do. ♀, P. | 18. 12. 11 |
| 147. ♂ | *Faureia milanjica* Karsch, ♀, P. | 25. 12. 11 |
| 148. ♀ | *Gastrimargus* sp. near *crassipes* Sjöst., ♂, P. | 13. 12. 11 |
| 149. ♂ | *Gymnobothrus linea-alba* Bol., ♂, C.P. | 26. 12. 11 |
| 150. ♀ | do. ♀, P. | 18. 12. 11 |
| 151. ♀ | do. ♂, P. | 23. 12. 11 |
| 152. ♀ | do. ♀, P. | 25. 12. 11 |
| 153. ♂ | *Heteracris speciosa* Sjöst., ♀, P. | 14. 12. 11 |
| 154. ♂ | do. ♂, P. | 28. 12. 11 |
| 155. ♂ | *Heteropternis couloniana* Sauss., ♀, C.P. | 20. 12. 11 |
| 156. ♂ | do. ♀, C.P. | 22. 12. 11 |
| 157. ♂ | do. ♀, C.P. | 23. 12. 11 |
| 158. ♂ | do. ♂, C.P. | 26. 12. 11 |
| 159. ♂ | do. ♀ | 3. 1. 12 |
| 160. ♀ | do. ♀, C.P. | 13. 12. 11 |
| 161. ♀ | do. ♀, C.P. | 26. 12. 11 |
| 162. ♀ | do. ♀, C.P. | 26. 12. 11 |
| 163. ♀ | do. ? sex, C.P. | 22. 12. 11 |
| 164. ♀ | do. ♂ | 28. 12. 11 |
| 165. ♂ | *H.* sp. ? *couloniana* Sauss. imm., ♀, P. | 16. 12. 11 |
| 166. ♂ | do. ♀, C.P. | 21. 12. 11 |
| 167. ♂ | *H. saussurei* Kirby, ♂, P. | 16. 12. 11 |
| 168. ♂ | do. ♀, P. | 19. 12. 11 |
| 169. ♀ | *Humbe tenuicornis* Schaum, ♂, C.P. | 16. 12. 11 |
| 170. ♀ | do. ♀, C.P. | 19. 12. 11 |
| 171. ♀ | do. ♂, P. | 27. 12. 11 |
| 172. ♀ | *Lentula candidoi* Ramme, ♂, C.P. | 13. 12. 11 |
| 173. ♂ | *Machaeridia* sp., ♂, C.P. | 21. 12. 11 |
| 174. ♂ | *Morphacris fasciata* Thunb., ♀, P. | 14. 12. 11 |
| 175. ♂ | *Orthochtha bisulcata* Krauss, ♂, C.P. | 26. 12. 11 |
| 176. ♀ | do. ♂, C.P. | 12. 12. 11 |
| 177. ♀ | do. ♂, C.P. | 12. 12. 11 |
| 178. ♀ | do. ♂, P. | 14. 12. 11 |
| 179. ♂ | *Ochrophlebia ligneola* Serv., ♂, P. | 14. 12. 11 |
| 180. ♂ | *Paracomacris productus* Walk., ♀, P. | 20. 12. 11 |
| 181. ♀ | do. ♀, P. | 14. 12. 11 |
| 182. ♂ | *Paraparga* sp., ♂, P. | 16. 12. 11 |
| 183. ♂ | do. ♂, P. | 29. 12. 11 |

Table 4 (*cont.*).

| | | | |
|---|---|---|---|
| | ORTHOPTERA (*cont.*) | | |
| 184. ♂ | *Parepistaurus* sp., ♂, C.P. | | 26. 12. 11 |
| 185. ♀ | *Pnorisa squalus* Stål, ♀, P. | | 14. 12. 11 |
| 186. ♂ | *Pyrgomorpha* sp., ? ♀, C.P. | | 13. 12. 11 |
| 187. ♀ | do. | ? ♀, C.P. | 13. 12. 11 |
| 188. ♀ | do. | ♂, C.P. | 13. 12. 11 |
| 189. ♂ | ? Pyrgomorphinae sp. imm., | ♂, C.P. | 12. 12. 11 |
| 190. ♀ | do. | ♀, C.P. | 13. 12. 11 |
| 191. ♀ | do. | ♀, P. | 14. 12. 11 |
| 192. ♂ | Tetriginae sp. indet., ♀, C.P. | | 13. 12. 11 |
| 193. ♂ | *Thisoicetrus pulchripes* Schaum, | ♂, C.P. | 13. 12. 11 |
| 194. ♂ | do. | ♂, C.P. | 20. 12. 11 |
| 195. ♂ | do. | ♂, C.P. | 21. 12. 11 |
| 196. ♂ | do. | ♂, C.P. | 22. 12. 11 |
| 197. ♂ | do. | ♂, C.P. | 22. 12. 11 |
| 198. ♂ | do. | ♂, C.P. | 23. 12. 11 |
| 199. ♂ | do. | ♂, C.P. | 26. 12. 11 |
| 200. ♂ | do. | ♂ | 28. 12. 11 |
| 201. ♀ | do. | ♂, C.P. | 12. 12. 11 |
| 202. ♀ | do. | ♂, C.P. | 19. 12. 11 |
| 203. ♀ | do. | ♂, C.P. | 21. 12. 11 |
| 204. ♀ | do. | ♂ | 28. 12. 11 |
| 205. ♀ | do. | ♂, P. | 12. 11 |
| 206. ♂ | do. | imm., ♂, C.P. | 16. 12. 11 |
| 207. ♂ | do. | imm., ♀, C.P. | 21. 12. 11 |
| 208. ♀ | do. | imm., ♀, C.P. | 12. 12. 11 |
| 209. ♀ | do. | imm., ♀, C.P. | 12. 12. 11 |
| 210. ♀ | do. | imm., ♂, C.P. | 12. 12. 11 |
| 211. ♀ | do. | imm., ♂, C.P. | 13. 12. 11 |
| 212. ♀ | do. | imm., ♀, C.P. | 13. 12. 11 |
| 213. ♀ | do. | imm., ♀, C.P. | 16. 12. 11 |
| 214. ♀ | do. | imm., ♂, C.P. | 19. 12. 11 |
| 215. – | do. | imm., ♀, | 27. 12. 11 |
| 216. ♂ | Genus near *Usambilla* Sjöst., ♂, C.P. | | 23. 12. 11 |
| 217. ♂ | *Zonocerus elegans* Thunb., imm., | ♀, C.P. | 13. 12. 11 |
| 218. ♂ | do. | ♂, C.P. | 13. 12. 11 |
| 219. ♂ | do. | ♂, C.P. | 19. 12. 11 |
| 220. ♂ | do. | ♂, C.P. | 20. 12. 11 |
| 221. ♂ | do. | ?, C.P. | 21. 12. 11 |
| 222. ♂ | do. | ♂, C.P. | 26. 12. 11 |
| 223. ♀ | do. | ♂, C.P. | 12. 12. 11 |
| 224. ♀ | *Zonocerus elegans* Thunb., imm., | ♀, C.P. | 12. 12. 11 |
| 225. ♀ | do. | ♂, C.P. | 13. 12. 11 |
| 226. ♀ | do. | ♀, C.P. | 16. 12. 11 |
| 227. ♀ | do. | ♂, C.P. | 19. 12. 11 |
| | Gryllidae | | |
| 228. ♀ | *Gryllus* sp., ♀, C.P. | | 16. 12. 11 |
| | Tettigonidae | | |
| 229. ♀ | *Homocoryphus* sp., ♀, P. | | 15. 12. 11 |
| 230. ♀ | *Tylopsis bilineolata* Serv., ♀, P. | | 14. 12. 11 |
| | ORDER INDET. | | |
| 231. ♀ | Prey missing, C.P. | | 12. 12. 11 |

PREY OF *NEOLOPHONOTUS RHODESIENSIS* HOBBY.

| | | |
|---|---|---|
| | COLEOPTERA | |
| | Scarabaeidae | |
| 1. ♀ | *Bolbocerus ornatellum* Perch, ♂, P. | 2. 3. 12 |
| 2. ♀ | do. ♂, P. | 2. 3. 12 |
| | DIPTERA | |
| | Asilidae | |
| 3. ♀ | *Hoplistomera serripes* Fab., ♀, P. | 18. 2. 12 |
| 4. ♀ | *Laxenecera* sp., ♀, P. | 21. 2. 12 |
| | Bombyliidae | |
| 5. ♂ | *Anthrax pithecius* Fab., ? ♂, P. | 5–20. 3. 12 |
| 6. ♀ | *Bombylius analis* Fab., ♂, P. | 5–20. 3. 12 |
| 7. ♀ | do. ♀, P. | 5–20. 3. 12 |
| 8. ♂ | *Lomatia pictipennis* Wied., ? ♀, P. | 11. 2. 12 |
| 9. ♂ | *Systoechus* sp., ♀, P. | 19. 2. 12 |
| | Syrphidae | |
| 10. ♂ | *Syrphus* sp., ♀, P. | 20. 2. 12 |
| | HEMIPTERA | |
| | Coreidae | |
| 11. ♀ | *Latimbus* sp., ♀, P. | 4. 3. 12 |
| | Lygaeidae | |
| 12. ♀ | *Lygaeus rivularis* Germ., ♀, P. | 5–20. 3. 12 |

Table 4 (*cont.*).

| | | |
|---|---|---|
| | HYMENOPTERA | |
| | Anthophoridae | |
| 13. ♂ | *Anthophora capensis* Friese, ♀, P. | 4. 3. 12 |
| 14. ♂ | do. ♀, P. | 5–20. 3. 12 |
| | Apidae | |
| 15. ♂ | *Apis mellifera unicolor* Latr., var. *adansoni* Latr., ☿, P. | 7. 2. 12 |
| 16. ♂ | do. ☿, P. | 20. 2. 12 |
| 17. ♂ | do. ☿, P. | 5–20. 3. 12 |
| 18. ♀ | do. ☿, P. | 12–13. 2. 12 |
| 19. ♀ | do. ☿, P. | 23. 2. 12 |
| | Braconidae | |
| 20. ♀ | *Iphiaulax* sp. ♀, P. | 11. 2. 12 |
| | Megachilidae | |
| 21. ♂ | *Megachile bituberculata* Rits., ♀, P. | 23. 2. 12 |
| 22. ♂ | *M. gratiosa* Gerst., ♀, P. | 23. 2. 12 |
| 23. ♂ | *M. consanguinea* Smith, ♂, P. | 25. 2. 12 |
| 24. ♀ | *M. cordata* Smith, ♀, P. | 20. 2. 12 |
| 25. ♂ | *M.* sp., ♀, P. | 22. 2. 12 |
| 26. ♂ | do. ♀, P. | 23. 2. 12 |
| 27. ♀ | do. ♀, P. | 2. 3. 12 |
| | Pompilidae | |
| 28. ♂ | *Pseudagenia* sp., ♂, P. | 15. 2. 12 |
| 29. ♀ | do. ♀, P. | 12–13. 2. 12 |
| | ORTHOPTERA | |
| | Acrididae | |
| 30. ♂ | *Acolopus thalassinus* Fab., ♂, P. | 5–20. 3. 12 |
| 31. ♂ | *Gymnobothrus linea-alba* Bol., ♀, P. | 5–20. 3. 12 |
| 32. ♀ | do. ♂, P. | 5–20. 3. 12 |
| 33. ♂ | *Paracomacris productus* Walk., ♀, P. | 25. 2. 12 |
| 34. ♂ | do. ♂, P. | 5–20. 3. 12 |
| 35. ♀ | do. ♂, P. | 5–20. 3. 12 |
| 36. ♂ | *Pseudochirista temporalis* Stål, ♂, P. | 15. 2. 12 |
| 37. ♀ | do. ♂, P. | 11. 2. 12 |
| 38. ♂ | *Trilophidia angustipennis* Kirby, ♂, P. | 5–20. 3. 12 |
| | ORDER INDET. | |
| 39. ♀ | Prey missing, P. | 5–20. 3. 12 |

PREY OF *MEROGYMNUS NIGROFLAVIPES* HOBBY.

| | | |
|---|---|---|
| | DIPTERA | |
| | Asilidae | |
| 1. ♀ | *Neolaparus* sp. D, ♀, P. | 21. 12. 11 |
| | Bombyliidae | |
| 2. ♀ | *Petrorossia* sp. ? *tenera* Loew, ♀, P. | 22. 2. 12 |
| | HEMIPTERA | |
| | Lygaeidae | |
| 3. ♀ | *Lygaeus rivularis* Germ., ♀, P. | 20. 2. 12 |
| | Cicadidae | |
| 4. ♀ | *Melampsalta* sp., ♂, P. | 27. 12. 12 |
| | HYMENOPTERA | |
| | Anthophoridae | |
| 5. ♀ | *Anthophora albigena fallax* Smith, ♂, P. | 17. 2. 12 |
| | Pompilidae | |
| 6. ♀ | *Salius tamisien* Guer., ♂, P. | 29. 12. 11 |
| | ORTHOPTERA | |
| | Acrididae | |
| 7. ♀ | *Gymnobothrus linea-alba* Bol., ♂, P. | 21. 2. 12 |
| 8. ♀ | do. ♂, P. | 2. 3. 12 |
| 9. ♀ | do. ♀, P. | 2. 3. 12 |
| 10. ♂ | *Orthochtha bisulcata* Krauss, imm., ♂, P. | 29. 12. 11 |
| 11. ♂ | *Paracomacris productus* Walk., ♀, P. | 25. 2. 12 |
| 12. ♀ | Pygomorphinae sp. indet. imm., ♀, P. | 14. 12. 11 |

PREY OF *SYNOLCUS AURULENTUS* ENGEL.

| | | |
|---|---|---|
| | ORTHOPTERA | |
| | Acrididae | |
| 1. ♀ | Eumastacinae sp. indet. imm., ♀, P. | 5. 1. 12 |

PREY OF ASILINE SP. INDET.

| | | |
|---|---|---|
| | DIPTERA | |
| | Asilidae | |
| 1. ♀ | *Neolaparus* sp. E, ♀, P. | 28. 12. 11 |

# A CENSUS OF SHORT-EARED OWLS (*ASIO F. FLAMMEUS*) AT NEWCASTLETON, ROXBURGHSHIRE, 1934[1]

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(*With Plate* 4 *and* 1 *Map in the Text.*)

## 1. Introduction.

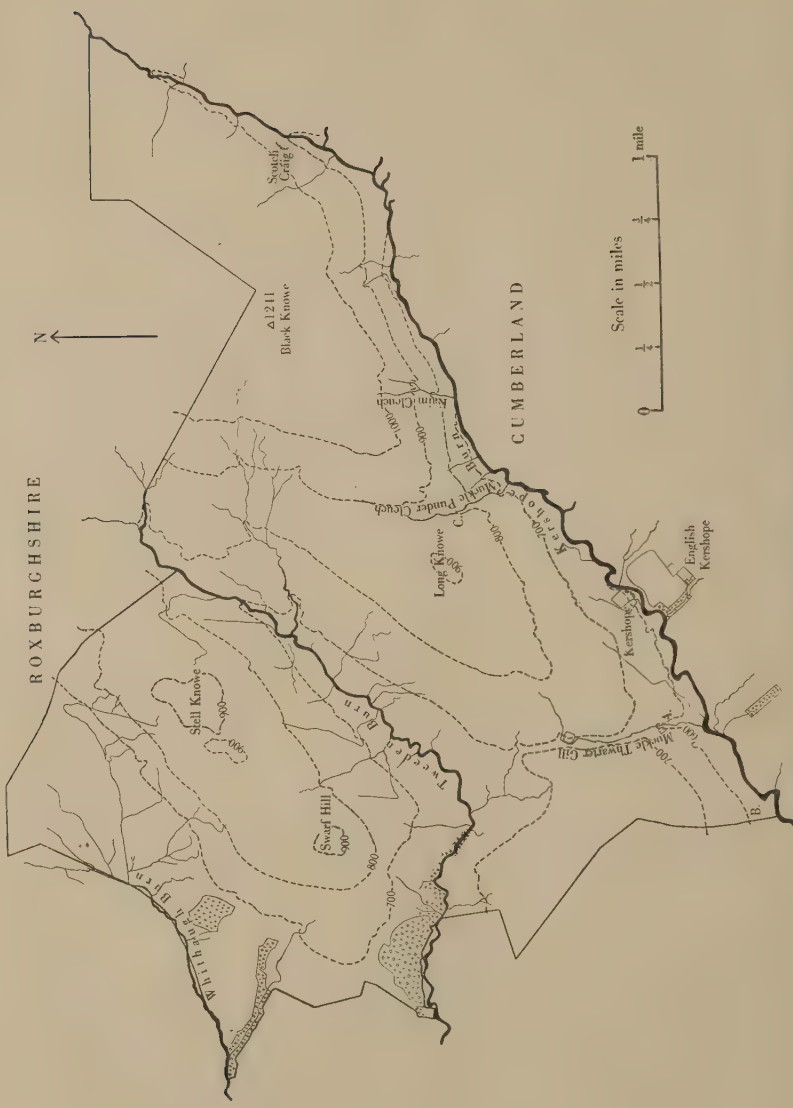
At the beginning of March 1934, I was asked by the British Trust for Ornithology to investigate the population of short-eared owls (*Asio f. flammeus* (Pontopp.)) on the State Forest at Newcastleton, in co-operation with the work which was being carried on by the Oxford University Bureau of Animal Population on fluctuations in the population of voles (*Microtus agrestis*) in that area. Part of the expense of my investigation was defrayed from a grant to Mr Charles Elton from the Royal Society, to whom acknowledgment is made. I desire to express my thanks to Mr John F. MacIntyre, the forester, for much kind help and to Mr James Murray and Mr Carruthers who have watched the nests, sent me reports, and shown an active interest in the work in various other ways.

Voles on the Border fluctuate rather regularly in numbers, reaching a maximum every three or four years. Previous general observations collected during the Oxford enquiry indicated that short-eared owls were regular visitors to Newcastleton, at any rate during years of vole abundance. It was anticipated that 1933 would probably be the peak year at Newcastleton, and that the voles would probably die off from epidemic disease during the spring of 1934. The relation of voles to the spring breeding of owls in 1934 promised therefore to be of special interest. An account of the vole work by Mr Elton and Dr G. M. Findlay, in which it is shown that these forecasts were correct, will appear later in this *Journal*.

## 2. The census area.

The State Forest at Newcastleton in Roxburghshire consists altogether of 3532 acres, and its elevation above sea-level varies between 500 and 1000 ft. It is divided into two parts known respectively as Tweedenhead and Dykecrofts. Tweedenhead, with an area of 2271 acres, is newly planted and is enclosed within sheep-proof fencing. Dykecrofts is open moorland and is at present unplanted and grazed by sheep. The Kershope Burn forms the boundary

[1] Publication of the British Trust for Ornithology.




Map of the Newcastleton Forest. A. Four owlets reared here. B. Owl sitting on seven addled eggs here. C. Clutch of seven eggs discovered here on March 22nd or 23rd.

of the forest on the east and south sides, and this burn is actually part of the Border between England and Scotland. The English side of the Kershope Burn is wild moorland partly given up to sheep-farming. Tweedenhead is eminently suitable ground upon which to carry out investigations into the relationships between owls and voles, for it is an enclosed ungrazed area which therefore provides good cover for voles and it is entirely surrounded by sheep pastures where the vole population is low. It is upon Tweedenhead that an attempt is being made to correlate the short-eared owl and vole populations, and the investigations will be carried out over a number of years.

On its southern side Tweedenhead slopes fairly steeply from 700 or 800 ft. down to the Kershope Burn which is 600 ft. above sea-level. On this southern side of the forest there are a number of gills or cleuchs running almost due south into the Kershope Burn. The sides of the gills and cleuchs slope more or less steeply and they are covered with grass (*Molinia caerulea*) and bracken (*Pteris aquilina*). There are also a number of patches of bracken here and there along the southern slope in between the gills and cleuchs. The southern slope of Tweedenhead is the most recently planted portion of the forest; planting, in fact, was still in progress in the spring of 1934. The trees on this area are only six or eight inches high, planted in upturned turfs. As planting on Tweedenhead has been in progress for more than ten years, the trees on some of the other areas are 6 ft. or more high and they are planted so closely together that the lower branches of one tree may touch those of another or even interlace. At the present time the southern slope of Tweedenhead is ideal country for short-eared owls. The birds when quartering the ground can see everything which moves beneath them, and the small newly-planted trees do not incommode them when they stoop and rise. Furthermore, the southern slope provides ideal nesting ground. The whole of this area is sheltered from the north, and the sides of the gills and cleuchs give shelter from the east and west and good cover can be obtained in the patches of bracken.

### 3. The owl census.

I paid my first visit to Newcastleton on April 14th, 1934, as I was informed that the short-eared owls had already started nesting, and I spent three days investigating Tweedenhead. The forester and one of his assistants took me to the sites of three nests which were known to them. Two of them were in Muckle Thwarter Gill and the third in Muckle Punder Cleuch. In Muckle Thwarter Gill we found an owl sitting on seven eggs. The other nest in this gill was deserted. I was told that there had been two or three eggs in it. The nest in Muckle Punder Cleuch was also deserted. When it was shown to me it contained one whole egg and broken shells of others were lying close by. The forester told me that this nest had contained seven eggs in the middle of March. As this appeared to me to be unusually early for the nesting of this species of owl, I asked him if he could give me the exact date. He said that he could because

his diary would contain a note of what the men were doing at that particular spot when they found the nest. He referred to his diary and said the date was either March 22nd or 23rd.

I spent the whole of April 15th, 16th and 17th looking for owls and searching for their nests. I saw several owls each day but could not find more than the one occupied nest. Nevertheless I came to the conclusion that there were probably three pairs of owls on the area with a possibility of a fourth. At first sight it may appear to be difficult to compute the number of pairs of owls on the area without marking down the nests but fortunately I discovered that there were two distinct colour forms of the short-eared owl on the forest. The female sitting in Muckle Thwarter Gill was a rich warm brown, whilst her mate was quite a cold grey. There was as much difference in the colour of these two birds as there is between the two extreme colour forms of the tawny owl (*Strix aluco*). The female was, at this time, sitting very closely, so closely, in fact, that she allowed me to approach within three yards of the nest before she left it. The male appeared to do his hunting within a radius of 300 or 400 yards of the nest, and when he was not hunting he was resting on a rock or upturned turf within 50 yards or so of the sitting female.

On several occasions I saw a pair of owls flying and hunting together on the northern slope of Tweedenhead, always in the same place, which was about three-quarters of a mile due north of the nesting site mentioned in the previous paragraph. Furthermore, both of these birds were of the grey form.

I saw, also, an owl of the brown form quartering the ground in the neighbourhood of Kaim Cleuch which is about a mile and a half north-east of the nesting site in Muckle Thwarter Gill. This bird was unlikely to be the brown female of Muckle Thwarter Gill who was sitting so closely and as it was always alone I assumed that it was a male and that it probably had a mate sitting either in one of the two branches of Kaim Cleuch or somewhere in the patches of bracken on the southern slope of the forest in that neighbourhood. I searched the whole of this area but was unable to find a nest.

The facts so far stated appear to me to be fairly good evidence for assuming that there were three pairs of short-eared owls on Tweedenhead. My assumption of the possibility of a fourth pair is based on evidence which is not so satisfactory. On April 16th, I was watching the grey pair of owls at about 50 yards range when I saw a third owl quartering the ground some distance away. The bird was a long way from me and I only saw it in flight but the sun was shining and it appeared to be warmer in colour than the two birds close to me. It was well outside of the normal range of the Muckle Thwarter Gill birds and even further away from Kaim Cleuch.

I returned to Newcastleton again on April 28th and spent the 29th and 30th and May 1st on Tweedenhead. On April 29th, there were three owlets and four eggs in the nest in Muckle Thwarter Gill and on April 30th another owlet hatched out. On May 13th I saw four owlets in this nest but when I went to

*Photo. T. Russell Goddard*

Phot. 1. Muckle Thwarter Gill, Newcastleton.

*Photo. T. Russell Goddard*

Phot. 2. Short-eared owl sitting.

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ring them on the following day the two elder ones had left the nest; however, I ringed the two which remained.

On May 1st I was taken by one of the forest workers to see another owl's nest which had been found close to the western boundary fence of Tweedenhead. This nest contained seven eggs, but when I touched them they were stone cold; and as I saw no owls in the neighbourhood I concluded that the nest was deserted. As one of the bystanders expressed a desire to have one of the eggs, I said that one might be taken but the remaining six eggs ought to be left in case the owls returned. I left Newcastleton the following morning but I visited this nest again on May 13th and much to my astonishment found a bird sitting. When it rose from the nest it disclosed seven eggs. The female had laid another egg to replace the one which was taken away on May 1st. One of the eggs was chipping. Both of the owls to which this nest belonged were of the brown form. This nest was approximately 860 yards from the one in Muckle Thwarter Gill. On June 12th I received a letter from Mr James Murray, one of the workers on the forest, in which he told me that he had visited this nest on the previous day, June 11th, and found one of the birds sitting on six eggs, the seventh having disappeared. He also said that he had shaken one or two of the eggs and they appeared to be rotten. There was not the slightest doubt about that for the bird to my knowledge had been sitting on a full clutch of eggs for 42 days and there is no doubt that she had been sitting for some time before I first saw her on May 1st.

On June 25th I received another letter from Mr James Murray telling me that when walking through one of the plantations on Tweedenhead he had disturbed five young owls. If he was correct in his assumption that all five were young birds of the year it would be definite proof that three pairs of short-eared owls had nested on Tweedenhead this year and that two families had been reared. On the other hand, if the five owls were really an adult female and four young they might easily have been the Muckle Thwarter Gill family. However, I have no reason to doubt the accuracy of Mr Murray's statement that all five were young birds of the year.

### 4. Desertion of nests.

The deserted nest which I was shown on the west side of Muckle Thwarter Gill on April 16th was, I think, a first attempt at nesting made by the pair of owls which eventually reared four young on the opposite side of the same gill. The deserted nest in Muckle Punder Cleuch, which had contained seven eggs on March 22nd or 23rd, was probably a first attempt made by a pair of owls which I suspected of having a nest in April somewhere in the neighbourhood of Kaim Cleuch, or it may have belonged to the pair which finally settled down, unfortunately without result, near to the western boundary fence of the forest. The question arises as to why these nests were deserted. I noticed that the forest workers were always accompanied by two sheep dogs, so I asked the

men how they discovered the owls' nests. As I expected, the reply was: "The dogs put the owls up." I think there is not the slightest doubt that whilst the men are working the dogs amuse themselves by harrying any owls which may be sitting in their neighbourhood. Special steps will have to be taken to prevent this happening in future.

## 5. Summary.

1. Short-eared owls (*Asio f. flammeus*) vary considerably in their general coloration during the breeding season. Some are brown and others are grey.

2. A short-eared owl was sitting on a clutch of seven eggs on March 22nd or 23rd—an early date.

3. There were at least three pairs of short-eared owls on Tweedenhead (2271 acres) during the breeding season of 1934, and the evidence collected appears to prove that two pairs reared young successfully. Both birds of one pair were of the brown form, in another pair both of the birds were grey and in the third pair the male was grey and the female a rich brown.

4. The pair of short-eared owls in which the male and female were markedly different in their general coloration were under close observation on many occasions between April 16th and May 14th and at various hours of the day. On no occasion was the male observed sitting on the eggs.

5. A short-eared owl was sitting on addled eggs for at least 42 days.

6. The maximum number of eggs in a clutch this year was seven.

## Reference.

**Goddard, T. Russell (1935).** "Notes on colour variation and habits of short-eared owl." British Birds, 28, 290–91.

# STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

## IV. THE ARABIS MIDGE, *DASYNEURA ARABIS* (CECIDOMYIDAE)

By H. F. BARNES.

(*Entomology Department, Rothamsted Experimental Station.*)

(*With Plate* 5 *and* 1 *Figure in the Text.*)

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### 1. Introduction.

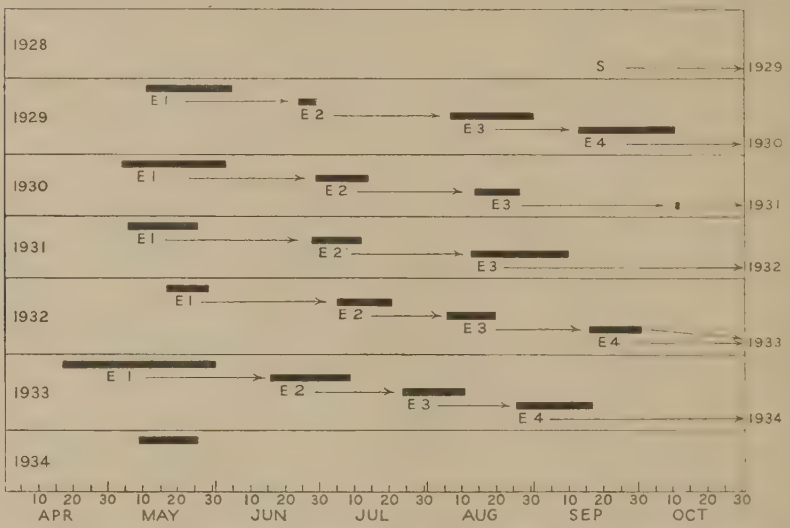
This is the fourth of a series of papers giving the results of an attempt to study fluctuations in insect populations. References to the earlier papers are to be found in the third study (**2**).

In the present contribution an account will be given of the Arabis midge (*Dasyneura arabis* Barnes), which has been kept under observation from the autumn of 1928 until the spring of 1934. This study differs fundamentally from the other ones in so far as the midge, a multi-brooded species, has been reared on *Arabis albida* continuously in captivity in an outdoor insectary ever since the original material was obtained in September 1928. Since then eighteen generations have passed. In the previous cases, i.e. when dealing with the wheat blossom midges, the foxtail midge (*D. alopecuri* Reuter) and the button top midge of willows (*R. heterobia* H.Lw.), it has been the custom to obtain fresh wild material for each generation to be investigated. The work in the present case has therefore resolved itself into an inquiry as to the varying dates of emergence and number of broods that occur in this species under insectary conditions, providing of course that plants in the right stage of growth are always available. This is important as in a state of nature the individuals emerging first in any flight might perish without leaving progeny, owing to lack of suitable plants.

### 2. Methods.

A sample of galled plants was obtained on September 18th 1928 from Godalming, Surrey, through the kindness of Mr H. Thackeray Turner and Mr G. Fox Wilson. The galls were cut off the plants and placed in a lamp glass over a pot containing fibre and soil. This pot was kept in an outdoor

insectary all through the winter. A few days after the midges started emerging in the spring (1929), a certain number of them were allowed to mate and were then placed in a muslin cage which contained an *Arabis* plant growing in a 10-in. pot. The remainder of the midges in the brood were killed on emergence. This artificial limitation of the egg-laying period is responsible for the apparent lack of overlapping of the various broods (Text-fig. 1). Such pots were kept in the same insectary. The midges oviposited on the living plant buds. From time to time the galls which developed were examined and, as soon as the larvae were seen to be nearly full grown or a cocoon was found, all the galls were cut off the plant and placed in a lamp glass cage. The majority of the




Text-fig. 1. Number of broods and emergence dates of *D. arabis* Barnes 1929–34. *s*, date of original wild sample; $E_1$, $E_2$, etc., dates of egg-laying allowed in first, second, etc., broods; the black lines represent the emergence periods of the adults of the various broods and the arrows connect the eggs with the resulting adult midges (see Table 2).

larvae and cocoons were so removed from the living plant cage; but a few midges always developed from larvae that had descended to the soil prior to the cutting of the galls. Such midges were counted and their daily emergences noted just the same as those in the lamp glass pots. The whole of this procedure was followed throughout the experiment, a totally new breeding cage being set up within the first few days of any flight of midges starting. In addition, sometimes some of the midges emerging from the soil in the old pot were allowed to remain in the cage and carry on for a further generation on the same plant. In such cases the time taken to complete a generation was found to be longer than when the midges oviposited on a fresh plant that had not been attacked immediately previous.

Phot. 2. Typical gall of *Dasyneura arabis*, Barnes, on *Arabis albida*. (*By courtesy of G. Fox Wilson, Esq., The Editor of the S.E. Agric. Coll. Wye Journal, and Messrs Headley Bros.*)



*Photo. V. S. Stansfield*

Phot. 1. Gall at base of flowering stem of *Arabis albida*, resulting in malformed shoot. A healthy flower shoot is to the right.

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There was a certain amount of difficulty in always having a new pot of *Arabis* ready in the right stage of plant growth. In the summer the plants are naturally inclined to send up flowering shoots; this had to be prevented and vegetative growth produced, since the larvae do not survive when eggs are laid on flower buds.

A few parasites emerged from the original wild sample but since then no parasites have occurred in the breeding cages. However, in 1931, larvae of the garden carpet moth (*Xanthorhoë fluctuata* Linn.) intruded and ate out several of the midge galls, apparently being particularly attracted to the terminal shoots. This probably caused some of the midge larvae to leave the galls prematurely. Again in 1933 larvae of the diamond back moth (*Plutella maculipennis* Curtis) were found in the breeding cages eating the *Arabis* leaves but doing no damage to the experiment. Frequently the aphid *Myzus persicae* Sulzer has appeared on the *Arabis* plants and occasionally the larvae of a gall midge (*Phaenobremia* sp.) which are predaceous on this aphid.

### 3. Bionomics.

*Name.* *Dasyneura arabis* Barnes was first described (**3**) in 1927 from specimens reared from galls on *Arabis albida* obtained at Byfleet, Surrey in November 1926. An earlier attack had been observed by Mr G. Fox Wilson at Wisley in 1922. Another midge, *D. schneideri* Rübs., doing similar damage to the same species of plant, yet differing in one or two structural characters, was described in 1917 from Zürich. It seems quite possible that in the future it will be proved that these two species are identical and that the differences observed between them fall within the range of variation. In this case the species would have to be known as *D. schneideri* Rübs.

*Damage.* The damage is characteristic, the centre growth of the shoots being galled (Pl. 5, phot. 2). Side branches arise as the consequence of this stoppage in the main terminal growth. The galls usually occur on the vegetative growing points, but sometimes the plant is attacked just as a flowering shoot is developing and then a very malformed flowering stem results (Pl. 5, phot. 1). In no case, however, have larvae been found galling the blossoms as might be expected.

*Development.* The eggs are red and are tucked away as deep as possible in the leaf buds among the hairs of the leaves. The larvae, which are sometimes white and sometimes pinkish, have the anterior extremities of the "anchor-process" rounded. They remain inside the gall throughout their feeding period. When full grown some leave the galls and pupate in the ground, others remain in the galls and spin white cocoons in which pupation takes place. Table 1 contrasts the numbers and sex ratios of midges emerging from galls with those developing from pupae in the soil. It will be seen that relatively more males emerged from the soil than from the galls. This is an interesting observation, since, owing to the method of cutting and removing the galls, it implies that

those larvae which develop the quicker and so have left the galls by the time cutting takes place are more likely to be males than females. This is in accord with the fact that the males are inclined to emerge before the females. However, the individuals remaining in the galls have usually started emerging a day or two before those in the soil. This is explicable if one takes into account the fact that the temperature in the galls during the summer is likely to be higher than that in the soil and so development of the pupae in the gall is probably slightly faster than that of those in the soil. As many as 98 larvae and cocoons have been found in a single gall. This particular gall was obtained from Godalming in August 1929. Usually, however, the number is nearer 20–30. The species has several broods a year, the last generation and occasionally part of the penultimate overwintering in their cocoons on the plants and in the soil.

Table 1. *Numbers and sex ratio of* D. arabis *emerging from soil and from galls.*

| | Emergences from galls | | Emergences from soil | |
|---|---|---|---|---|
| | Numbers | | | Numbers |
| Brood | ♂ ♀ | Sex ratio | Sex ratio | ♂ ♀ |
| 1932 First brood | 82–246 | 25 : 75 | 48 : 52 | 301–332 |
| Second brood | (i) 161–473 | 25 : 75 | 50 : 50 | 118–114 |
| ,, | (ii) 82–192 | 30 : 70 | 50 : 50 | 82– 81 |
| 1933 First brood | (i) 75–145 | 34 : 66 | 66 : 34 | 63– 32 |
| ,, | (ii) 145–187 | 44 : 56 | 57 : 43 | 50– 38 |
| Second brood | (i) 280–948 | 23 : 77 | 36 : 64 | 97–169 |
| ,, | (ii) 141–400 | 26 : 74 | 46 : 54 | 43– 51 |
| ,, | (iii) 111–360 | 24 : 76 | 23 : 77 | 30–101 |
| ,, | (iv) 99–277 | 26 : 74 | 48 : 52 | 39– 43 |

*Host plant.* The only known host plant of this species is *Arabis albida*. A report was received that this midge was also attacking *Aubretia*. In experiments set up to verify this, the midges readily laid eggs on the terminal shoots, flower buds and calyx of open flowers of *A. leichtlina* and mixed *Aubretia*. The shoots turned brown and died, presumably owing to the action of the young larvae; but as the plants did not react and form galls the larvae were not able to survive. The plants gave rise to side shoots. In a later year a further report of damaged *Aubretia* was received; in this case the "*Aubretia*" turned out to be *Arabis albida* when actual specimens were received. A further trial was made, using *Cerastium tomentosum* plants. The midges readily laid eggs which hatched. But again, the plants did not react, no galls were formed and the larvae died. Kieffer (**4**) described in 1909 the gall of a midge he named *D. alpestris* from Central Europe. This species makes a similar gall on *Arabis alpina* and *A. hirsuta*. These plants have not yet been tested as possible host plants of *D. arabis*.

*Enemies and parasites.* Predaceous gall midge larvae have been found feeding on the larvae of *D. arabis*. They have been reared and are a species

of *Lestodiplosis* (Barnes coll. Nos. 585 ♀, 1140 ♂). One parasite has been reared from *D. arabis* larvae: *Misocyclops marchali* K. I am indebted to Dr Ferrière of the Imperial Institute of Entomology for having identified it for me.

### 4. Number of broods and emergence dates.

For the sake of clarity, it may be stated that when discussing the number of broods in a year, a brood is considered to belong to the year in which the eggs were laid and the larvae developed, and not necessarily to the year in which the resulting adults emerged. The number of midge flights in a year will usually be the same as the number of broods, the first flight being that of the last brood of the previous year and the last flight being that of the penultimate brood. Occasionally, as in 1930, there will be one more flight or partial flight than the number of broods. In that year there were four flights and only three broods. This was due to the fact that there was a partial flight of the third brood, the majority of which were not on the wing till the following year. Normally an additional brood would result from a flight of midges.

This species has several broods a year and the number that occurred during the years 1929–1933 can be easily read off from Text-fig. 1, as well as the number of flights in any particular year. Thus in 1931 there were three broods of which the last overwintered as full grown larvae; in 1930 there were also three broods, but one individual of the last brood emerged in October. In 1932 there were four broods; part of the third brood and the entire fourth brood did not emerge until 1933. Thus the first flight in 1933 was composed of part of the 1932 third brood and the entire 1932 fourth brood. In 1929 and 1933 there were also four broods; in these two years the entire third brood emerged the same year. In no year has any of the fourth brood emerged the same year as the eggs were laid. Under natural conditions when all the adults of a brood would oviposit, there would be considerable overlapping owing to the length of the flight period in the various broods. It must be realised however that each individual midge only lives about 48 hours and completes oviposition in that period.

Table 2. *Dates of first and last emergence in the broods of* D. arabis 1929–34.

| Brood Year | Overwintering* | First | Second | Third |
|---|---|---|---|---|
| 1929 | May 11–1st week in June | June 24– ? | Aug. 7–31 | Sept. 13–Oct. 11 |
| 1930 | May 4–June 3 | June 29–July 14 | Aug. 14–27 | Oct. 11† |
| 1931 | May 6–26 | June 28–July 12 | Aug. 13–Sept. 10 | — |
| 1932 | May 17–29 | July 5–21 | Aug. 6–20 | Sept. 16–1st week in Oct. |
| 1933 | Apr. 17–May 31 | June 16–July 9 | July 24–Aug. 11 | Aug. 26–Sept. 17 |
| 1934 | May 9–26 | — | — | — |

* Consists of the adults of the third or fourth or third and fourth broods of the previous year.
† One individual only.

The emergence dates of the various broods can be seen on reference to Text-fig. 1 and Table 2. The earliest date of emergence is seen to be April 17th and the latest is October 11th. In spite of small variations in the dates from year to year, the outstanding feature is the constancy with which an almost complete levelling up takes place by the end of any year, even in a hot one like 1933.

### 5. Sex ratio.

In a previous paper (1) it was concluded that in this species there are male-producing families and female-producing families in addition to families which produce individuals of both sexes in approximately equal numbers. A further conclusion was that the occurrence of unisexual families was not usual. A test was made in 1932 in order to see whether the time of fertilisation of the females after emergence had any effect on the sex ratio. Females were mated within 2 hours of emergence, about 6–7 hours after, about 24 hours after and about 48 hours after emergence. The results are given in Table 3. Mr F. Yates, who has kindly examined the figures, tells me that there is a difference which is just significant between the sex ratios of the families resulting from females mated within 2 and after 6–7 hours of emergence compared with those of females mated 24 and 48 hours after emergence. More males are produced when the females are old at the time of fertilisation. There is also confirmation of what was found previously, namely that there are male-producing families and female-producing families.

Table 3. *Result of delayed mating on the sex ratio of* D. arabis.

| Time of mating | Numbers of males and females in resulting families |
|---|---|
| 6 ♀♀ mated within 2 hours of emergence | 5–27; 12–15; 3–35; 7–18; 1–6; 4–12 |
| 5 ♀♀ mated about 6–7 hours after emergence | 1–6; 1–24; 6–15; 1–2; 8–16 |
| 8 ♀♀ mated about 24 hours after emergence | 3–11; 9–19; 3–10; 0–0; 1–0; 7–5; 7–3; 3–0 |
| 7 ♀♀ mated about 48 hours after emergence | 9–5; 0–0; 6–35; 0–0; 4–5; 12–11; 0–0 |

Table 4. *Sex ratio and numbers of* D. arabis, 1929–33.

| Year | ♂♂ | ♀♀ | Total | Sex ratio |
|---|---|---|---|---|
| 1929 | 242 | 601 | 843 | 29 : 71 |
| 1930 | 351 | 681 | 1032 | 34 : 66 |
| 1931 | 260 | 891 | 1151 | 23 : 77 |
| 1932 | 887 | 1763 | 2650 | 34 : 66 |
| 1933 | 1410 | 4376 | 5786 | 24 : 76 |
| 1929–33 | 3150 | 8312 | 11462 | 27 : 73 |

The fact that delayed fertilisation appears to send up the numbers of males is most interesting. Naturally in the field such a state would almost never obtain, the females being fertilised very soon after emergence. The sex ratios of the *Arabis* midges which have been reared in the course of this fluctuation study are shown in Table 4. One reason for giving this table is to show that mass breeding of this midge will not give a 50 : 50 ratio. It will be seen that over the whole period the ratio is 27 : 73. Mating has occurred in all cases

soon after emergence. In the former experiments when the midges were mated 24 and 46 hours after emergence there were several cases in which more than 50 per cent. males occurred; when the females were mated 2 hours and 6–7 hours after emergence the percentage of males was usually in the twenties.

In Table 5 the sex ratios of the separate broods are shown. It will be seen that in the overwintering brood of 1932-3 the percentage of females is extraordinarily high. No explanation of this is possible at present. On the whole the first brood of the year seems to have the highest percentage of males, the second brood less and the third and overwintering broods the least. It may be that temperature is the underlying factor controlling the rate of segmentation of the unfertilised eggs and so determining the extent of development of the egg at the time of entry of the sperm. When segmentation is rapid (warm weather) the egg is in an older state by the time the male impregnates the female than when segmentation is slow. If the state of development of the egg at fertilisation, rather than the age of the female, influences the percentage of males in the resulting family, one would expect a higher percentage of males in the warmer weather. But the reverse is found. As the season advances so the percentage of males decreases. Differential mortality may be the *raison d'être* of these rather queer sex ratios.

Table 5. *Sex ratio of different broods of* D. arabis.

| Brood | | Sex ratio | Total emergences ♂ | Total emergences ♀ |
|---|---|---|---|---|
| Overwintering | 1928–29 | 16 : 84 | 14 | 70 |
| ,, | 1929–30 | 25 : 75* | 149 | 450 |
| ,, | 1930–31 | 25 : 75† | 91 | 275 |
| ,, | 1931–32 | 17 : 83‡ | 34 | 168 |
| ,, | 1932–33 | 4 : 96§ | 3 | 80 |
| ,, | 1932–33 | 3 : 97‖ | 10 | 337 |
| ,, | 1933–34 | 23 : 77¶ | 55 | 187 |
| First brood | 1929 | — | — | — |
| ,, | 1930 | 51 : 49 | 164 | 159 |
| ,, | 1931 | 34 : 66 | 58 | 116 |
| ,, | 1932 | 40 : 60 | 383 | 578 |
| ,, | 1933 | (i) 44 : 56 | 138 | 177 |
| ,, | 1933 | (ii) 46 : 54 | 195 | 225 |
| Second brood | 1929 | 22 : 78 | 62 | 224 |
| ,, | 1930 | 34 : 66 | 37 | 72 |
| ,, | 1931 | 18 : 82 | 111 | 500 |
| ,, | 1932 | (i) 32 : 68 | 279 | 587 |
| ,, | 1932 | (ii) 38 : 62 | 164 | 273 |
| ,, | 1933 | (i) 25 : 75 | 377 | 1117 |
| ,, | 1933 | (ii) 29 : 71 | 184 | 451 |
| ,, | 1933 | (iii) 23 : 77 | 141 | 461 |
| ,, | 1933 | (iv) 30 : 70 | 138 | 320 |
| Third brood | 1929 | 35 : 65 | 155 | 294 |
| ,, | 1932 | 15 : 85§ | 27 | 157 |
| ,, | 1933 | (i) 17 : 83 | 115 | 554 |
| ,, | 1933 | (ii) 15 : 85 | 108 | 632 |

* Fourth brood 1929. † Third brood 1930 with exception of one ♂ which emerged in 1930.
‡ Third brood 1931 § Partial emergence of third brood 1932. ‖ Fourth brood 1932.
¶ Fourth brood 1933.

## 6. Summary.

1. This is the fourth of a series of papers in which the fluctuations of insect populations are being studied. It deals with *Dasyneura arabis* Barnes.

2. The bionomics of this species receive attention.

3. The dates of emergence and the number of broods when bred under insectary conditions during the period 1928–34 are given. The constancy with which the minor variations caused by differences in weather conditions become levelled out by the end of the year is notable.

4. Delayed fertilisation of the females appears to send up the numbers of males in the ensuing family. The sex ratios of the various broods are different. As the season advances the percentage of males decreases.

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# A RECONNAISSANCE OF WOODLAND BIRD COMMUNITIES IN ENGLAND AND WALES

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## 1. Introduction.

This paper records the results of an enquiry carried out in connection with a series of National Broadcast talks in the spring of 1933. Surveys of woodland birds were made during the nesting season in May and June 1933, by observers at twenty-five points. Although I have assembled the results, the field work is entirely theirs, and I take this opportunity of thanking them for the care and enthusiasm with which they did these surveys; also the British Broadcasting Corporation, and in particular Mrs Mary Adams, for their courtesy and the facilities extended; and Mr W. B. Alexander for advice and for allowing me the use of some bird census figures collected by him and by the Oxford University Ornithological Society.

## 2. Questionnaire.

A questionnaire was published in the *Listener*, and explained in one of the talks (see Elton, 1933). It is reproduced below:

1. *Name and address* (including county and nearest town).

2. *Types of wood chosen.* For each of the three types of wood, (*a*) oak, (*b*) beech, and (*c*) pine, give the following information:

(1) Local name.

(2) Situation (approximate height above sea level, nearest town, etc.).

(3) Approximate size (acreage or dimensions).

(4) Nature of surrounding country (heath, pasture, arable, etc.).

(5) Undergrowth (bramble, bracken, hazel, holly, etc.).

(6) Soil (clay, sand, etc.).

(7) Special characteristics (whether visited by people, under smoke influence, preserved for game, or near sea coast).

(8) Do grey squirrels occur?

(9) Do wood ant nests occur?

(10) Dominant tree.

*Note:* Choose nature woods which are as far as possible of one pure type, (*a*), (*b*) or (*c*), and not plantations or mixed woods. If the wood does not conform to the three main types give detailed description. As there are two different kinds of oak tree which grow on different soils please send for identification a dozen stalked oak leaves chosen from different trees.

3. *Birds.* Give a complete list of the birds living in each of three types of wood, (*a*), (*b*) and (*c*), during May and June. Mark nesting birds *N*; mark birds seldom seen *R*. Make a special note if any of the observations are not your own, or if they refer to other months than May and June.

### 3. Surveys.

Several observers sent in reports that contained useful information but were insufficient for comparative purposes. These included, as it happened, the two replies from Scotland and the one from Ireland, so that discussion is mainly limited to stations in England and Wales, of which a list is given in Table 1, together with the relevant details about habitats. The original letters, lists, etc., have been deposited with the British Trust for Ornithology at Oxford, for the use of future investigators, who it is hoped will be able to carry out more detailed enquiries than the broadcast method allows.

In the following table the items occur in this order: observer, wood, nearest town or village, county, situation, height above sea, size, dominant trees, (other trees), dominant undergrowth, (other undergrowth), subsoil, surrounding habitats, human interference, presence of grey squirrels and wood ants. These items are not all given for every station.

Table 1. *Descriptions of woods in England and Wales in which surveys were made during May and June* 1933.

1. G. M. Stanford. *Burwood, Cranborne, Dorset*, 300 *ft.*, 108 *acres, oak* (*s. and p.**) 2/3, *ash* 1/3 (sweet chestnut, sycamore, birch). Hazel, bramble, bracken (sallow, privet, dogwood). Chalk (patches of clay, gravel, sand). Arable and wood. Preserved, public footpath, little disturbed. No G.S. or W.A.
2. A. Nicholls. *Whitewebbs Woods, Enfield, Middlesex*, 150 *ft.*, 102 *acres, oak* (*p.*) *and hornbeam* (horse chestnut, birch, pine, lime). Bramble, bracken (rosebay in June, July), young birch. London clay. Pasture. Formerly closed, opened as public wood since 1932, much frequented. G.S. not seen, but occurs near. No W.A.
3. N. M. Drage and students of Bangor Normal College. *Siliwen, Bangor, Caernarvonshire, on slopes of Menai Straits*, 75–100 *ft.*, *c.* 40 *acres, oak* (*s.*). Bramble, rose, hazel, ivy, bilberry, holly, sycamore and ash saplings, oak scrub. Shale. Pasture, houses and wood near. Public path much used in summer. No G.S. or W.A.
4. M. Longbottom. *Hirst Wood, Saltaire, Yorkshire, bottom of Aire Valley*, 250 *ft.*, 30 *acres, oak* (*p.*). Birch and beech subdom. (sycamore, elm). Bracken, bluebells, grasses. Sandy loam. River, canal, railway cutting. Much visited by public, no game preservation, near sewage works. No G.S. or W.A.
5. R. H. Nelson. *Sandy Balls Wood, Godshill, Hampshire*, 200–300 *ft.*, 100 *acres, pine* (40 *acres*), *oak* (20 *acres*), *beech* (10 *acres*), *mixed* (30 *acres*). Bramble and bracken. Sand, clay, gravel. Arable, river and water meadows, heath (New Forest). Campers in summer. No G.S. (red S. occur). W.A. numerous. Birds are recorded for A, pine; B, oak; C, beech.
6. Wellington College Natural History Society.
   A. *Breach Copse, Wokingham, Berkshire*, 200 *ft.*, 2 *acres, oak* (*p.*), chiefly mature, not decayed enough for woodpeckers. Bramble, bracken, hazel (very thick). Gravel. River meadows with hedges and oaks. Game preserved, not frequented, no smoke. G.S. and W.A. occur.
   B. *Palmer's Lake Wood, ditto*, 12 *acres, pine*. Little undergrowth, some bracken and heather, birches and sweet chestnuts. Gravel. Pinewoods mixed with heath. Frequently visited, no game preserved, no smoke. G.S. and W.A. abundant.
7. R. P. Overend, K. O. Kellett and A. Douglas. *Jagger Park* (*Royds Hall Wood*), *Bradford and Halifax, Yorkshire*, 2½ *miles long, with stream running through*, 700–800 *ft.*, *c.* 400 *acres, beech*. Bramble, bracken, holly (hazel); some second growth after War cutting; bilberry and heather on part burnt in 1921. Clay over shaly sandstone. Pasture and meadow. No game preserved; frequented but not much disturbed; mills and coal mines around. No G.S. (or red). W.A. abundant.
8. R. A. Billen. *High Wood, Lytchett Matravers near Wareham, Hampshire*, 200–250 *ft.* 200 *acres, oak* (*s. and p.*). Bracken, bramble (hazel), bluebells, etc. Clay. Parkland, meadow, arable. Game preserved; not frequented. No G.S. or W.A.

* *Quercus sessiliflora* or *Q. robur* (*pedunculata*).

Table I (*cont.*).

9. R. Atkinson.
A. *Wood near Henley-on-Thames, Oxfordshire,* 350–400 *ft.,* 4 *acres, oak* (*p.*) (cherry, and beech hedge). Hazel, bramble, bracken, maple, young ash. Flinty clay over chalk. Meadows and beech woods. Not much frequented. G.S. occur. No W.A.
B. *Ditto,* 1–2 *acres, beech* (cherry, elm). Little undergrowth, bramble, holly. Clay with flints. Pasture with woods. Little frequented. Probably G.S. occur. No W.A.
C. *Whitehanging Plantation, ditto,* 15 *acres, larch, pine, spruce.* Young larches, some bramble, many dead fallen larches. Chalk on flinty clay. Pasture with woods. Game preserved and little visited up to 1933. G.S. occur. No W.A.

10. K. L. Tivendale and members of Muswell Hill Zoological Society.
A. *Hadley Wood, Barnet, Middlesex,* 325 *ft.,* 86 *acres, oak and beech.* Holly (hawthorn). London clay. Pasture. Frequented; no smoke. G.S. occur. No W.A.
B. *Highgate Wood, Highgate, Middlesex,* 320 *ft.,* 100 *acres, oak* (*p.*). Little undergrowth (holly). London clay. Houses (7 miles from open country). Much frequented; under smoke influence. G.S. occur. No W.A.
C. *Coldfall Wood, Finchley, Middlesex, c.* 300 *ft.,* 30 *acres, oak* (*p.*). Much undergrowth (hawthorn, bracken, bramble, hazel, osiers near stream). London clay. Allotments and houses (6 miles from open country). Frequented by a few people; under smoke influence. No G.S. or W.A.

11. D. Wrightman. *Broom Hill, Ipswich, Suffolk* (*on hill above town*), 10 *acres, pine.* Bracken and grass. Sand. Pasture, scrub, road. Fairly frequented. No G.S. or W.A.

12. W. S. Marshall. *Parkside Wood, Leeds, Yorkshire,* 4–5 *acres, beech* (*oak, pine*). Little undergrowth except some holly, bramble, etc. Clay. Arable, pasture, gardens, game not preserved, public, much frequented. G.S. occur. No W.A.

13. Z. Croad. *Royal Inn Wood, Portsmouth, Hampshire,* 140 *ft.,* 35 *acres, oak* (*p.*). Bramble, blackthorn, hazel, hawthorn, bracken, grass. Light loam. Pasture, arable, woods. Game preserved. No G.S. or W.A.

14. J. K. W. Wheatley.
A. *North part of Prince's Coverts, Epsom, Surrey,* 100 *ft.* (*large area*), *oak* (*p.*). Hazel, holly, bramble, ash saplings. Clay. Pasture and arable, and wood. Not much frequented. G.S. occur. No W.A.
B. *Oxshott Heath and Esher Common, ditto* (*large area*), *pine.* The area shows succession stages following War cutting (see Summerhayes, Cole and Williams, 1924). Bramble, bracken. heather. Sand. Much frequented. G.S. few. W.A. numerous.

15. H. E. Irwin. "*The Glen*", *St Leonards-on-Sea, Sussex, ravine with a stream,* 200 *ft., c.* 4 *acres, oak* (*p.*) (beech, ash, alder, elm, lime, conifers). Small trees, many decayed. Hazel (holly, bramble, laurel, rhododendron), not very thick. Clay. Houses and gardens. Little disturbed, but many cats. No game preserved. Some smoke. G.S. occur. No W.A. seen, though abundant near.

16. W. B. Alexander and Oxford Ornithological Society.
A. *Bushy Copse, Sandford, Oxfordshire,* 200 *ft.,* 4 *acres, oak* (*p.*). Patches of blackthorn thicket, otherwise little undergrowth. Clay. Pasture. No game preserved, not much frequented except for periodic bird censuses. G.S. occur. No W.A.
B. *Bassemer Copse.* 1 acre; undergrowth some elders. Arable and pasture. Otherwise as in "A".
C. *Slipe Copse,* 1 acre, undergrowth dense elders. Otherwise as in "A".
D. *Swan's Copse,* 3 acres, undergrowth sedges and brambles, visited by campers from River Thames. Otherwise as in "A".

## 4. CONCLUSIONS.

The birds recorded from these 27 woods are listed in Table 2, which also contains some Finland data from Palmgren (1930) for comparison: *N* means definite evidence of nesting; *R* means rare; *ordinary brackets* indicate that the species is recorded from the wood margin; *square brackets* indicate a record for some period previous to May and June 1933. Thus every symbol represents some form of positive record. Birds of the swallow tribe and swifts have been omitted from the lists. These surveys are almost certainly incomplete in some cases; in others the woods are too small or too uniform to contain representatives

Table 2. *Results of woodland bird surveys.* 1–15, *B.B.C. surveys.* 16 *a–d, Oxford Bird Census.*

| Species recorded in the British surveys | 1 | 2 | 3 | 4 | 5a | 5b | 5c | 6a | 6b | 7 | 8 | 9a | 9b | 9c | 10a | 10b | 10c |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rook (*Corvus frugilegus*) | × | . | . | . | . | . | . | . | . | *N* | . | . | . | . | × | . | . |
| Carrion crow (*C. corone*) | . | . | . | . | . | . | . | *N* | *N* | . | . | . | . | . | × | *R* | × |
| Jackdaw (*Coloeus monedula*) | × | × | . | . | . | . | . | . | . | [*R*] | × | . | . | . | × | . | . |
| Jay (*Garrulus glandarius*) | *NR* | × | . | . | . | *N* | . | *N* | . | . | *R* | . | . | *N* | *N* | *N* | × |
| Magpie (*Pica pica*) | . | . | . | *R* | . | . | . | *N* | . | *N* | . | . | . | . | . | . | . |
| Starling (*Sturnus vulgaris*) | × | *N* | . | *N* | . | *N* | *N* | . | *N* | × | *N* | × | *N* | . | *N* | × | × |
| Goldfinch (*Carduelis carduelis*) | . | . | . | . | *R* | . | . | . | . | . | . | . | . | . | . | . | . |
| Lesser redpoll (*C. linaria*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × |
| Linnet (*C. cannabina*) | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . |
| Bullfinch (*Pyrrhula pyrrhula*) | *N* | *R* | . | . | *RN* | . | . | . | . | . | . | . | . | *N* | . | . | × |
| Greenfinch (*Chloris chloris*) | . | (×) | *N* | *R* | . | *R* | . | . | . | × | . | . | . | . | . | . | . |
| Hawfinch (*Coccothraustes coccothraustes*) | (*NR*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Chaffinch (*Fringilla cselebs*) | *N* | × | *N* | *N* | *N* | . | . | *N* | . | *N* | *N* | × | × | *N* | × | *N* | *N* |
| *Sparrow (*Passer* sp.) | . | *N* | . | × | . | . | . | . | . | [×] | . | × | . | . | × | *N* | × |
| Yellow bunting (*Emberiza citrinella*) | . | . | . | *N* | . | . | . | . | . | [×] | *N* | . | . | . | . | . | . |
| Cirl bunting (*E. cirlus*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Reed bunting (*E. schoeniclus*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Tree pipit (*Anthus trivialis*) | . | . | . | *N* | . | . | . | . | . | × | . | . | . | . | *N* | . | . |
| Yellow wagtail (*Motacilla flava*) | . | . | . | . | . | . | . | . | . | [×] | . | . | . | . | . | . | . |
| Grey wagtail (*M. cinerea*) | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . |
| Pied wagtail (*M. alba yarrellii*) | . | . | *N* | (*N*) | . | . | . | . | . | . | . | . | . | . | . | . | × |
| Tree-creeper (*Certhia familiaris*) | *N* | . | . | . | *N* | *N* | . | × | . | . | . | . | . | . | × | . | . |
| Nuthatch (*Sitta europaea*) | *N* | . | . | . | *NR* | . | . | . | . | . | . | . | . | . | × | . | . |
| Great tit (*Parus major*) | *N* | × | . | *N* | *N* | . | . | *N* | × | × | *N* | × | × | × | *N* | *N* | *N* |
| Blue tit (*P. caeruleus*) | *N* | *N* | . | *N* | *N* | . | . | *N* | . | × | . | × | . | × | *N* | *N* | *N* |
| Coal tit (*P. ater*) | *N* | × | *N* | . | . | . | . | . | × | [*R*] | *N* | . | . | × | × | . | . |
| *Marsh or willow tit (*P. palustris* or *atricapillus*) | *NR* | × | . | . | . | . | . | . | . | . | *N* | *N* | . | × | *R* | . | *R* |
| Long-tailed tit (*Aegithalos caudatus*) | *N* | *R* | . | . | *N* | . | . | *N* | . | . | . | [*N*] | . | . | . | . | . |
| Goldcrest (*Regulus regulus*) | × | . | . | . | *R* | . | . | . | × | . | . | . | . | . | . | . | . |
| Spotted flycatcher (*Muscicapa striata*) | *N* | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . |
| Chiffchaff (*Phylloscopus collybita*) | *N* | × | *N* | . | *N* | . | . | . | . | . | *N* | . | . | . | . | . | *R* |
| Willow warbler (*P. trochilus*) | *N* | × | *N* | *N* | . | . | . | *N* | . | [×] | *N* | *N* | . | . | *N* | × | *N* |
| Wood warbler (*P. sibilatrix*) | × | . | *N* | . | *N* | . | . | . | . | × | . | . | . | . | . | . | . |
| Garden warbler (*Sylvia borin*) | × | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | × |
| Blackcap (*S. atricapilla*) | × | × | . | . | *N* | . | . | . | . | . | . | × | . | . | × | . | . |
| Whitethroat (*S. communis*) | × | *N* | . | . | . | . | . | *N* | . | . | *N* | × | . | . | × | . | × |
| Lesser whitethroat (*S. curruca*) | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . |
| Mistle thrush (*Turdus viscivorus*) | *N* | × | . | *N* | *NR* | . | . | . | . | × | *N* | *N* | *N* | . | × | × | × |
| Song thrush (*T. philomelus*) | *N* | *N* | *N* | *N* | *N* | . | . | *N* | . | *N* | *N* | *N* | *N* | *N* | *N* | *N* | *N* |
| Blackbird (*T. merula*) | *N* | × | *N* | *N* | *N* | . | . | *N* | . | *N* | *N* | *N* | *N* | *N* | *N* | *N* | *N* |
| Redstart (*Phoenicurus phoenicurus*) | . | *R* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Nightingale (*Luscinia megarhyncha*) | *N* | (×) | . | . | *R* | . | . | . | . | . | *NR* | . | . | . | × | . | . |
| Robin (*Erithacus rubecula*) | *N* | . | *N* | *N* | *N* | . | . | *N* | × | *N* | *N* | *N* | *N* | *N* | *N* | *N* | *N* |
| Hedge sparrow (*Prunella modularis*) | *N* | . | *N* | *R* | . | . | . | . | . | . | *N* | × | × | *N* | × | × | × |
| Wren (*Troglodytes troglodytes*) | *N* | × | *N* | . | *N* | . | . | . | . | *N* | *N* | *N* | × | . | *N* | . | × |
| Nightjar (*Caprimulgus europaeus*) | *N* | . | . | . | . | . | . | . | . | . | × | × | . | × | . | . | . |
| Green woodpecker (*Picus viridis*) | *R* | (*R*) | . | . | *N* | *N* | . | . | *N* | [×] | *R* | [*R*] | × | × | × | . | . |
| Great spotted woodpecker (*Dryobates major*) | *N* | *R* | . | [*N*] | *NR* | . | . | . | . | . | . | . | . | . | × | *N* | *N* |
| Lesser spotted woodpecker (*D. minor*) | *R* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Wryneck (*Jynx torquilla*) | . | . | . | . | *R* | . | . | . | . | . | . | . | . | . | . | . | . |
| Cuckoo (*Cuculus canorus*) | . | × | . | . | . | × | . | . | . | × | × | . | . | . | × | × | × |
| Wood pigeon (*Columba palumbus*) | *N* | *N* | *N* | . | *N* | . | *N* | *N* | *N* | *N* | *N* | × | *N* | *N* | *N* | *N* | *N* |
| Stock dove (*C. oenas*) | *N* | . | . | . | . | . | . | . | . | . | . | *N* | × | . | . | . | × |
| Turtle dove (*Streptopelia turtur*) | . | × | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . |
| Woodcock (*Scolopax rusticola*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Moorhen (*Gallinula chloropus*) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Pheasant (*Phasianus colchicus*) | *N* | . | . | . | . | . | *N* | *N* | . | . | . | . | . | × | . | . | . |
| Common partridge (*Perdix perdix*) | *N* | . | . | . | . | . | . | . | . | [*R*] | . | . | . | . | . | . | . |
| Little owl (*Athene noctua*) | × | . | . | . | . | *N* | . | . | . | . | . | . | . | . | . | . | . |
| Long-eared owl (*Asio otus*) | *N* | . | . | . | . | . | *N* | . | . | . | . | . | . | . | . | . | . |
| Tawny owl (*Strix aluco*) | . | × | . | . | . | . | . | . | . | *N* | *N* | . | . | × | . | . | . |
| Barn owl (*Tyto alba*) | *R* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Sparrowhawk (*Accipiter nisus*) | *N* | . | . | . | . | . | . | . | *N* | [×] | . | . | . | × | . | . | . |
| Kestrel (*Falco tinnunculus*) | . | . | . | . | . | . | . | *N* | . | [×] | . | . | . | . | × | . | . |
| Total number of species recorded | 41 | 28 | 13 | 17 | 22 | 7 | 4 | 16 | 9 | 30 | 26 | 20 | 12 | 17 | 31 | 17 | 25 |

*For symbols see text. Names follow British Check-list, and (for Finland) Palmgren's paper.*

| 11 | 12 | 13 | 14*a* | 14*b* | 15 | 16*a* | 16*b* | 16*c* | 16*d* | No. of records | Deciduous woods | Conifer woods | Finland: Mixed woods with scrub | | Finland: Conifer woods | | Birds peculiar to the Finland lists (*) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| × | . | . | . | × | *N* | . | . | . | . | 6 | × | × | . | | . | | |
| . | . | . | . | . | . | × | . | . | × | 8 | × | × | . | | × | | Hooded crow (*Corvus cornix*) |
| × | *R* | . | . | *N* | *N* | . | × | . | . | 11 | × | × | × | * | . | * | Nutcracker |
| . | *N* | *N* | . | *N* | *R* | × | . | . | . | 14 | × | × | . | | | * | (*Nucifraga caryocatactes*) |
| . | *R* | × | . | . | . | × | . | . | . | 6 | × | . | × | | . | | |
| × | . | *N* | . | *N* | *N* | . | × | × | . | 19 | × | × | × | | × | | |
| × | . | . | . | . | *N* | . | . | . | . | 3 | × | × | | * | | * | Siskin (*C. spinus*) |
| . | . | . | . | . | . | . | . | . | . | 1 | × | . | . | | . | | |
| × | . | . | . | . | . | × | . | . | . | 3 | × | × | . | | . | | |
| . | . | *N* | . | . | *N* | . | . | . | . | 7 | × | × | × | | × | | |
| × | × | *N* | . | . | *N* | . | . | × | . | 10 | × | × | . | | . | | |
| . | . | *N* | . | . | *N* | . | . | . | . | 3 | × | . | . | | . | | |
| *N* | × | *N* | *N* | *N* | *N* | × | × | × | × | 23 | × | × | × | | × | | |
| *N* | × | × | . | . | *N* | . | × | . | . | 12 | × | × | . | | . | | |
| × | . | *N* | . | *R* | . | . | . | . | × | 7 | × | × | . | | . | | |
| . | . | *N* | . | . | . | . | . | . | . | 1 | × | . | . | | . | | |
| . | . | . | . | *N* | . | . | . | . | . | 1 | . | × | . | | . | | |
| . | . | . | (*R*) | *N* | . | . | . | . | × | 6 | × | . | . | | . | | |
| . | . | . | . | . | . | . | . | . | . | 1 | × | . | . | | . | | |
| . | . | . | . | . | . | . | . | . | . | 1 | × | . | . | | . | | |
| . | . | . | . | . | (*R*) | . | . | . | . | 4 | × | × | . | | . | | |
| × | . | *N* | . | . | *N* | × | . | . | × | 10 | × | × | × | | × | | |
| × | . | *N* | . | . | . | . | . | . | . | 5 | × | . | . | | . | | |
| *N* | *N* | . | *R* | *N* | *N* | . | × | × | × | 22 | × | × | × | | × | | |
| × | *R* | *N* | *N* | *N* | *N* | × | . | × | × | 20 | × | × | × | | . | | |
| *N* | . | *N* | . | . | *N* | . | . | . | × | 12 | × | × | × | | × | | |
| . | . | *N* | . | *R* | *N* | × | . | × | × | 13 | × | × | × | | × | | Willow tit (Finland) |
| . | . | *N* | *R* | × | *N* | . | . | . | × | 10 | × | × | × | | . | | |
| . | . | . | . | . | *N* | . | . | . | . | 4 | × | × | × | | × | | |
| . | . | *N* | . | . | *N* | . | . | . | × | 5 | × | × | × | * | × | * | Pied flycatcher (*M. hypoleuca*) |
| . | . | *N* | . | . | *N* | × | × | × | × | 12 | × | × | × | | × | | |
| × | . | *N* | *NR* | *N* | *N* | × | . | . | × | 18 | × | × | × | | . | | |
| . | . | . | . | . | . | . | . | . | . | 4 | × | × | × | | × | | |
| . | . | *N* | . | . | *N* | × | . | × | × | 8 | × | . | × | | . | | |
| . | . | *N* | . | . | *N* | × | . | . | × | 9 | × | × | × | | . | | |
| × | . | *N* | *N* | . | *N* | × | . | × | × | 14 | × | . | . | | . | | |
| × | . | *N* | . | . | . | . | . | × | . | 4 | × | × | × | | . | | |
| × | *R* | *N* | . | . | *N* | . | . | × | . | 16 | × | × | . | | × | | |
| × | × | *N* | *N* | *NR* | *N* | × | × | × | × | 24 | × | × | × | * | × | * | Redwing (*T. musicus*) |
| × | × | *N* | *N* | *NR* | *N* | × | × | × | × | 24 | × | × | × | * | × | | Fieldfare (*T. pilaris*) |
| . | × | . | . | . | . | . | . | . | . | 2 | × | . | × | | . | | |
| . | . | [*N*] | . | × | *N* | × | . | . | . | 9 | × | × | . | | . | | |
| × | *N* | *N* | *N* | *N* | *N* | × | × | × | × | 24 | × | × | × | | × | | |
| × | *N* | *N* | . | × | *N* | × | × | . | × | 18 | × | × | . | | . | | |
| *N* | × | *N* | . | × | *N* | × | × | . | × | 18 | × | × | . | | × | | |
| . | . | *N* | . | . | . | . | . | . | . | 5 | × | × | . | | . | | |
| × | *R* | *N* | . | *N* | *N* | × | . | × | × | 19 | × | × | . | | . | | |
| . | . | *N* | . | . | . | . | . | . | . | 8 | × | × | × | * | × | * | Great black woodpecker |
| . | . | . | . | . | *R* | . | . | . | . | 2 | × | . | × | | . | | (*Dryocopus martius*) |
| . | . | . | . | . | . | . | . | . | . | 1 | . | × | . | | . | | |
| × | × | × | . | × | × | . | × | . | × | 14 | × | × | . | | × | | |
| *N* | *N* | *N* | *R* | *N* | *N* | × | × | × | × | 25 | × | × | × | | × | | |
| . | . | . | . | . | *N* | . | . | . | . | 5 | × | × | × | | . | | |
| × | . | *N* | . | . | . | . | . | . | × | 5 | × | × | . | | . | | |
| . | . | *N* | . | . | . | . | . | . | . | 1 | × | . | × | * | × | * | Green sandpiper |
| . | . | *N* | . | . | . | . | . | . | . | 1 | × | . | . | | . | | (*Tringa ochropus*) |
| . | . | *N* | . | × | . | . | . | . | × | 7 | × | × | . | * | . | | Black grouse (*Lyrurus tetrix*) |
| . | . | . | . | × | . | . | . | . | . | 3 | × | × | . | | . | | |
| . | . | *N* | . | . | *R* | . | . | × | . | 5 | × | . | . | | . | | |
| . | . | . | . | . | . | . | . | . | . | 2 | × | . | . | | . | | |
| × | *RN* | *N* | . | . | *R* | . | × | . | . | 9 | × | × | . | | . | | |
| . | . | × | . | . | *R* | . | . | . | . | 3 | × | . | . | | . | | |
| . | . | *N* | . | . | . | . | . | . | . | 5 | × | × | × | | . | * | Goshawk (*Accipiter gentilis*) |
| × | *R* | × | . | . | *R* | × | . | . | . | 8 | × | × | . | | . | * | Common buzzard (*Buteo buteo*) |
| 29 | 20 | 44 | 11 | 24 | 40 | 21 | 15 | 17 | 26 | . | 62 | 47 | 29 | 8 | 21 | 9 | |
| | | | | | | | | | | | | | 37 | | 30 | | |

of all species. They are in fact random samples studied by observers of differing skill and opportunity. We must, therefore, allow for two kinds of error that may affect individual surveys. First, some species may have been overlooked: this applies probably to several of the warblers (e.g. blackcap, wood warbler, etc.), and to some other species such as the hawfinch and lesser spotted woodpecker. Secondly, some species may have been wrongly identified: this applies possibly to some records of sparrows (house or tree), and probably to the marsh and willow tits*. Although it is certain that *some* records of these species are correct, I have refrained from specifying them. These species are marked with an asterisk. As might be expected, the larger lists came mostly from larger woods. Certain broad conclusions can be drawn from these surveys.

(1) *Value of habitat records.* The records, whatever generalisations we make from them here, form the first attempt to record detailed habitats of a large sample of woodland birds in England. They therefore represent an advance upon the type of field knowledge which remains locked inside the brains of ornithologists, which consequently dies with them, and which has in the past led to the frequent statement in handbooks that "this species occurs in every suitable habitat". The adequate description of bird habitats, though it presents serious difficulties and problems of its own, at any rate requires a basis of objective examples.

(2) *Number of species.* The lists vary from 4 (obviously incomplete) to 44. Most of them contain between 11 and 31 species, which we may take to be about the normal number of bird species to be expected in an English wood of 2–10 acres in size. This result agrees fairly closely with Palmgren's much more elaborate surveys in Finland (1931), which show the following numbers of species: savannah or meadow woodland ("Laubwiesen") 26, scrub woodland 38, mixed wood with scrub 37, mixed conifers 30, rock-pine woodland 25. The most universally distributed species appear to be the chaffinch, great tit, blue tit, song thrush, blackbird, robin, and wood pigeon. But it has to be remembered that small birds are subject to considerable fluctuations in numbers. If a survey had been taken in 1918 after the severe winter of 1917–18, tits might have appeared one of the rarest types of birds.

(3) *Effect of woodland types.* The summary in Table 2 proves that there is not much difference in species composition between the bird communities of deciduous woods (mainly oak, also beech, etc.) and conifer (mainly pine) woods. The 21 deciduous woods had at least 62 species and the 5 pine woods at least 47. As there is a considerable margin of species only recorded once or twice, or not true woodland dwellers (e.g. moorhens), this difference is not very significant, especially when the larger number of deciduous woods surveyed is taken into account. It was suggested by Hudson (1918) that pinewoods have a poor bird fauna, and it is possible that this was an impression gained from a lower *density* of birds. It remains to be seen whether English pinewoods have such a

* The Oxford records are certainly house sparrows and marsh tits.

lower density than deciduous woods, but this was certainly the case in the Finnish woods investigated by Palmgren, who recorded 1060 birds per sq. km. in mixed woodland with scrub, and only 400 per sq. km. in mixed conifer woodland. The fact that the scrubland had also 1060 birds per sq. km. suggests the great importance of undergrowth in increasing bird density, a fact which has already been widely recognised by makers of bird sanctuaries.

It cannot be said that oak woods and pine woods have exactly the same species of birds. No doubt there are a few which prefer deciduous (? garden warbler, tree-pipit, nuthatch, woodcock) and others that prefer pine (e.g. goldcrest). These points can only be settled by frequency counts. Thorpe (1925) has pointed out that pine woods in Scotland have certain distinctive species among which are crested tit (*Parus cristatus*), goldcrest, siskin (*Carduelis spinus*), crossbill (*Loxia curvirostra*), capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*), long-eared owl and sparrowhawk.

(4) *The woodland bird community.* It seems clear that we have in England and Wales one bird community, which shows minor variations in different types of woods, but is on the whole very constant in species, though not in densities and would appear more so if our woods were not in such small units. There is little doubt that the greatest changes occur during the development of plantations into high woods, especially with little undergrowth. Some of these changes have been recorded in their early stages by Lack (1933) working on the Breckland in Norfolk and earlier on by Brock (written 1913–14, published 1921). Although conditions may differ a little in Scotland, it seems likely that the change over from hardwood (deciduous) to conifer woodlands, that is happening on an enormous scale in this country under the pressure of economic demands, will not cause any very dramatic change in the woodland birds as a whole, although by causing more pronounced age-grouping of trees it will tend to split up birds into subcommunities during succession in a manner not usually found in mature, self-perpetuating woods. As Brock has remarked (1921, p. 53), "In a natural wood no such succession occurs. The wood has a stable character, conserved through natural seeding and the avifauna is likewise stable, or at least only subject to the ebb and flow never entirely absent in bird life". This statement is not strictly true, but illustrates a broad difference between natural and planted woods.

(5) *Antiquity of the woodland bird community.* Table 2 includes for comparison two of Palmgren's Finland bird communities and it can be seen that there is not a great deal of difference between them and the English ones. Certain northern species (redwing, fieldfare, nutcracker, siskin, great black woodpecker, etc.) come in, and certain southern species (nuthatch, nightingale, hedge-sparrow, etc.) fall out. This similarity extends to the few other surveys of woodland bird communities that have been made in Europe (e.g. Schiermann, 1930, 1934). We may conclude, therefore, that the British woodland birds form part of a very widespread life-zone extending eastwards into Asia. That they

are not recent arrivals is shown by the fact that no fewer than sixteen species are listed as British subspecies—implying a fairly long residence and isolation in this country (Witherby, 1924). These sixteen species, comprising nearly half the woodland bird community and the bulk of the resident species, are the jay, bullfinch, tree-creeper, six species of tits, nuthatch, goldcrest, song thrush, hedge-sparrow, robin, greater and lesser spotted woodpecker, and the tawny owl. In addition there are several formerly woodland birds which have formed special races on some of the wind-swept outer islands: the Shetland wren and starling, St Kilda wren and Hebridean thrush.

(6) *Niches in the woodland bird community.* There is a high degree of resemblance in the structure of such bird communities right round the world. Table 3 compares the birds of conifer woods in England, Finland and California (the Sierra Nevada). The Californian list has been worked out from the life-zone table and the habitat description for each species, given by Grinnell and Storer (1924). Although the species differ, there are usually representatives of the same ecological niches in each community, and some of the genera (*Sitta* the nuthatch, *Regulus* the goldcrest, *Nucifraga* the nutcracker) are actually the same in all these woodlands.

(7) *Habitat choice.* In its distinctness and richness of species, apparent antiquity and well-marked ecological structure, the woodland bird community of Britain has a parallel in the equally clearly demarcated community of birds living in the mountain forests of East Africa studied by Moreau (1933) who believes that these communities also are rather old and that the birds choose their surroundings for psychological reasons largely unconnected with adaptation and survival, although some species may become by association closely linked with certain niches in the woodland habitat. Lack (1933) has brought forward very strong evidence along the same lines for some British birds.

## 5. Summary.

1. A National Broadcast enquiry into woodland bird-life was made in 1933. The results of surveys in 23 woods are recorded. These are compared with available figures for the Oxford Bird Census and for Finland.

2. Woodland birds in Britain form a clear-cut and ancient community that is much the same in different woodland types (taking dominant trees as the index). It forms part of a life-zone widely spread over Europe.

3. The number of species of regular woodland birds in this country is in the neighbourhood of 30. There is a definite series of ecological niches that is the same in widely separated countries.

4. Present afforestation changes (increase of planted conifers) will not much affect the species found, but may bring about lower densities and a redistribution of species in different succession stages of vegetation.

Table 3. *The structure of conifer woodland bird communities in three different countries.*

| Sierra Nevada: conifer forests of the Hudsonian zone (after Grinnell and Storer, 1924) | Finland: mixed conifers (after Palmgren, 1931) | Britain: 5 pinewoods (B.B.C. survey) |
|---|---|---|
| | Carrion crow | Rook |
| | | Carrion crow |
| | Jackdaw | Jackdaw |
| | Jay | Jay |
| Clark nutcracker* | Nutcracker | |
| | Starling | Starling |
| Pine siskin | Siskin | |
| Pine grosbeak | | Goldfinch |
| | | Linnet |
| | Bullfinch | Bullfinch |
| | | Greenfinch |
| | Chaffinch | Chaffinch |
| Chipping sparrow | | Sparrow |
| Sierra junco | | Yellowhammer |
| | Treecreeper | Treecreeper |
| Red-breasted nuthatch* | | Nuthatch |
| Short-tailed mountain chickadee | Great tit | Great tit |
| | | Blue tit |
| | Coal tit | Coal tit |
| | Marsh tit | Marsh or willow tit |
| | | Long-tailed tit |
| Ruby-crowned kinglet* | Goldcrest | Goldcrest |
| Wood pewee | Spotted flycatcher | Spotted flycatcher |
| | Pied flycatcher | Tree pipit |
| Audubon "warbler" | Chiffchaff | Chiffchaff |
| | | Willow warbler |
| | Wood warbler | Wood warbler |
| | | Blackcap |
| | | Whitethroat |
| | | Lesser whitethroat |
| Western "robin" | Mistle thrush | Mistle thrush |
| | Song thrush | Song thrush |
| | Redwing | |
| | Blackbird | Blackbird |
| | | Nightingale |
| | Robin | Robin |
| | | Hedge sparrow |
| | Wren | Wren |
| Pacific nightjar | | Nightjar |
| Williamson sapsucker | | Green woodpecker |
| | Great spotted woodpecker | Great spotted woodpecker |
| Arctic 3-toed woodpecker | Great black woodpecker | |
| Modoc woodpecker | | Wryneck |
| | Cuckoo | Cuckoo |
| | Wood pigeon | Wood pigeon |
| | | Stock dove |
| | | Turtle dove |
| | Green sandpiper | |
| | Woodcock | |
| Sierra grouse | | Pheasant |
| | | Partridge |

* European genus.

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# THE POPULATION OF PARTRIDGES (*PERDIX PERDIX*) IN 1933 AND 1934 IN GREAT BRITAIN

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## 1. Introduction.

This paper is a comparative review of the population of partridges in 1933 and 1934, the period over which the present investigation has so far continued. This work forms part of a scheme of research on game populations carried out in the Bureau of Animal Population, Oxford University, with the aid of a grant from Imperial Chemical Industries.

During 1931 and 1932 the partridge population was greatly reduced by an outbreak of disease due to the parasitic worm (*Trichostrongylus tenuis* (**1**)). This was especially prevalent in the densely stocked areas of Hampshire and East Anglia where the birds had reached a very high density as a result of two favourable seasons in 1929 and 1930. It seems reasonable to regard 1932 as a minimum point in the periodic fluctuation which has been shown to exist in partridge numbers (**2**), and on this assumption it seemed probable that 1933 and 1934 would show a general increase in numbers. The records of nests, counts, and numbers killed which are given in this paper are published through the courtesy of estate owners, shooting men and keepers, without whose help such work would be impossible. Many owners do not like to have their names or the names of their estates published, so I have referred to all of them throughout by the index letter and number used in the files of the Bureau, together with the name of the county in which the estate is situated. In some cases the records refer to one part rather than the whole of a very large estate.

## 2. Nesting.

The result of the disease and unfavourable weather in 1931 and 1932 was a very sparse breeding stock for 1933. Except for one or two isolated instances (a few birds dying from Trichostrongylosis and pneumonia in Suffolk (C 10) Norfolk (W 1) Hampshire (L 4)) disease and heavy parasitism of any kind was practically absent from the old birds during the nesting season of 1933, and the weather conditions over most of England were considered to be more favourable than for many years past. The results of the nesting for 1933 and 1934 on estates in various parts of the country are compared in Table 1 which gives the details as far as known of nests, clutches and broods on 15 estates in 1933 and 20 in 1934; for 9 of these estates comparable records have been obtained

Table 1. *Records of nesting and hatching of partridges,* 1933 *and* 1934.

| 1933 Estate and county | Approx. acreage | Nests: Estimated total | Nests: Number found | Nests: Hatched | Nests: % hatched | Eggs and young: Av. clutch size | Eggs and young: Av. brood size | Eggs and young: % eggs hatched | Eggs and young: Estimated total young |
|---|---|---|---|---|---|---|---|---|---|
| L 1, Hampshire | 1100 | 40 | 30 | 27 | 90 | 14·2 | — | 90 | 460 |
| W 6, ,, | 2000 | 90 | 77 | 66 | 86 | 14·7 | 13·4 | 91 | 1019 |
| F 1, Wiltshire | 5000 | 140 | 100 | 59 | 59 | 15·1 | 14·0 | 93 | 1160 |
| C 1, Cambridgeshire | 900 | 60 | 37 | 31 | 84 | 16·4 | 14·8 | 90 | 748 |
| S 1, ,, | 11000 | 650 | 585 | 518 | 88 | 15·2 | 13·3 | 88 | 7700 |
| B 4, Warwickshire | 2700 | — | 38 | 27 | 71 | 13·8 | — | — | — |
| H 1, Worcestershire | 1700 | 70 | 16 | 11 | 69 | 16·1 | 15·4 | 95 | 742 |
| D 2, Northamptonshire | 5000 | — | 34 | 26 | 76 | 16·6 | 15·9 | 96 | — |
| B 2, Yorkshire | 2000 | 80 | 64 | 39 | 61 | 13·9 | 12·5 | 90 | 610 |
| L 2, Northumberland | 2000 | 100 | 30 | 20 | 66 | 15·1 | — | — | — |
| M 1, ,, | 830 | 40 | 25 | 22 | 88 | 14·0 | 13·0 | 93 | 458 |
| R 2, Hampshire | 4000 | 220 | 197 | 175 | 89 | 15·0 | 14·0 | 94 | 2745 |
| R 3, Wiltshire | 3000 | 160 | 143 | 116 | 81 | 13·7 | 12·4 | 90 | 1610 |
| B 1, Oxfordshire | 1500 | 80 | 66 | 56 | 85 | 14·5 | 12·7 | 86 | 864 |
| R 6, Lincolnshire | 1000 | 50 | 25 | 19 | 76 | 15·2 | 13·3 | 87 | 505 |
| Averages | | | | | **78** | **15·1** | **13·7** | **91** | |

| 1934 Estate and county | Approx. acreage | Nests: Estimated total | Nests: Number found | Nests: Hatched | Nests: % hatched | Eggs and young: Av. clutch size | Eggs and young: Av. brood size | Eggs and young: % eggs hatched | Eggs and young: Estimated total young |
|---|---|---|---|---|---|---|---|---|---|
| L 1, Hampshire | 1100 | 52 | 47 | 33 | 70 | 14·2 | — | — | — |
| W 6, ,, | 2000 | 100 | 69 | 58 | 84 | 14·1 | 12·9 | 90 | 1082 |
| F 1, Wiltshire | 5000 | 170 | 150 | 137 | 91 | 15·7 | 14·8 | 94 | 2700 |
| C 1, Cambridgeshire | 900 | 90 | 68 | 61 | 90 | 17·4 | 16·3 | 94 | 1320 |
| S 1, ,, | 11000 | 950 | — | — | — | 15·5 | 14·6 | 95 | — |
| B 4, Warwickshire | 2700 | — | 59 | 47 | 80 | 15·8 | — | — | — |
| H 1, Worcestershire | 1700 | 70 | 20 | 14 | 70 | 15·2 | 14·4 | 94 | 705 |
| D 2, Northamptonshire | 5000 | — | 41 | 29 | 71 | 14·8 | 13·6 | 92 | — |
| B 2, Yorkshire | 2000 | 90 | 79 | 46 | 58 | 15·8 | 14·6 | 94 | 761 |
| L 2, Northumberland | 2000 | 125 | 57 | 41 | 72 | 13·9 | 13·5 | 94 | 1218 |
| M 1, ,, | 830 | 70 | 39 | 30 | 77 | 14·4 | 13·5 | 94 | 729 |
| C 5, Isle of Wight | 2500 | 120 | 77 | 52 | 68 | 15·7 | 14·8 | 95 | 1215 |
| M 2, Hampshire | 2700 | — | 27 | 25 | 93 | 15·0 | 14·1 | 94 | — |
| L 8, Berkshire | 1700 | 180 | 153 | 125 | 82 | 14·5 | 13·8 | 95 | 2040 |
| C 10, Suffolk | 2000 | 166 | 157 | 146 | 93 | 15·9 | 13·9 | 87 | 2150 |
| W 11, Norfolk | 1400 | 110 | 101 | 76 | 76 | 15·6 | 14·4 | 93 | 1208 |
| W 1, ,, | 1400 | 150 | 133 | 116 | 87 | 14·9 | 14·2 | 95 | 1860 |
| D 4, Lincolnshire | 1000 | 95 | 92 | 72 | 78 | 15·3 | 13·8 | 90 | 1130 |
| H 10, Shropshire | 1500 | — | 75 | 43 | 57 | 15·4 | 14·7 | 95 | — |
| A 2, Derbyshire | 640 | 30 | 18 | 15 | 83 | 14·2 | 13·4 | 93 | 334 |
| | | | | | **78** | **15·2** | **14·2** | **93** | |

for both years. The estimates of the total number of nests on each area are the only figures in the table not derived from direct counts, but these estimates were made very carefully in consultation with the keepers at the end of the nesting season and are based on numbers of pairs seen, as well as on nests found. It is unlikely that there can be an error of as much as 10 per cent. in any of these figures, while in many cases there is every reason to believe that they are quite accurate. All the records utilised in this paper refer to game preserves which are well looked after, one keeper being employed to about every 1000–1500 acres. The number of nests hatched (fourth column) refers to those hatched out of the number found (third column).

The average clutch size, brood size and percentage of eggs hatched are derived from the same figures—the eggs laid and hatched in nests which successfully hatched under natural conditions. No clutches artificially incubated to the chipping stage under the "Euston System" are included in these figures. The estimates of the total number of young produced are calculated from the total nests, percentage of nests known to hatch and average brood size.

From this table it will be seen that on most areas 1934 was a more productive nesting season than 1933. If the various averages and percentages are averaged for each year (which practice I have adopted because I believe it gives a truer reflection of the real "average" than the gross averages) the figures for 1934 are nearly all more favourable than for 1933.

| | % nests hatched | Av. clutch | Av. brood | % eggs hatched |
|---|---|---|---|---|
| 1933 | 78 | 15·1 | 13·7 | 91 |
| 1934 | 78 | 15·2 | 14·2 | 93 |

The total number of nests in 1934 was greater than in 1933, as a more adequate breeding stock was left after the 1933–4 shooting season than survived from 1932. If the comparable figures are extracted from Table 1 it will be seen that on 9 estates with a combined area of 26,530 acres there were 1270 nests in 1933 and 1717 in 1934, an increase of 35 per cent. From field observation and other estimates it seems certain that the average of a more representative number of estates would show a much greater increase than this. The increase in nests was especially noticeable on some of the Norfolk estates, none of which are included in this selection of 9. Generally speaking, both 1933 and 1934 were exceptionally favourable nesting and hatching seasons in most districts, the weather being warm and dry throughout May and June, although local thunderstorms at hatching time caused some losses of broods and chicks. The loss of nests due to weather, predators, disturbance, farm operations, etc. in these and other years will be dealt with fully in another paper.

Table 2. *Counts of old and young partridges made in August* 1933.

| Estate and county | Estimated total nests | Count in August | | | | Young : old ratio | % coveys surviving | Av. young per covey | Stock estimate | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Old | Young | Coveys | "Barren" | | | | Young | Total |
| L 1, Hampshire | 40 | 68 | 318 | 25 | 18 | 4·68 | 74 | 12·7 | 375 | 455 |
| C 1, Cambridgeshire | 60 | 90 | 372 | 34 | 22 | 4·14 | 76 | 10·9 | 496 | 616 |
| S 1, ,, | 650 | 121 | 245 | 25 | 71 | 2·02 | 41 | 9·8 | 2630 | 3930 |
| W 1, Norfolk ,, | — | 75 | 226 | 29 | 17 | 3·01 | 77 | 7·8 | — | — |
| D 2, Northamptonshire | — | 212 | 650 | 68 | 78 | 3·07 | 64 | 9·6 | — | — |
| O 1, Nottinghamshire | 471 | 154 | 584 | 53 | 48 | 3·80 | 65 | 11·0 | 3580 | 4522 |
| B 2, Yorkshire | 80 | 65 | 226 | 23 | 19 | 3·48 | 71 | 9·8 | 557 | 717 |
| S 3, ,, | — | 21 | 61 | 8 | 5 | 2·90 | 76 | 7·6 | — | — |
| L 2, Northumberland | 100 | 88 | 434 | 39 | 10 | 4·93 | 89 | 11·0 | 987 | 1187 |
| Comparable averages: | | | | | | **3·56** | **70** | **10·0** | | |
| B 1, Oxfordshire | 80 | 117 | 87 | 19 | 79 | 0·74 | 33 | 4·6 | 128 | 288 |
| N 1, Yorkshire | 34 | 26 | 103 | 9 | 8 | 3·96 | 69 | 11·4 | 269 | 337 |

### 3. Counts in august.

With the exception of a few second nests made after the destruction of first nests, nearly all partridges hatch during the month of June. From hatching until the young birds are about a month old it is very difficult to make complete observations: in July all ground vegetation, corn crops, etc., form a dense cover and the partridge broods spend most of their time out of sight. This is the period when high mortality takes place among the young chicks, the causes of which will be discussed elsewhere. When the young birds are about three to four weeks old (towards the end of July or early in August) they are more frequently seen at the edges of cornfields and on mown hayfields, particularly in the early morning. On most areas it is then possible to see and count a reasonable sample of the population, since nearly all the coveys will rise when disturbed and it is very easy to distinguish young from old birds. A system of sample counting has been carried out during the first ten days of August in 1933 and 1934. I am deeply indebted to Mr W. J. Barry for his advice and experience in this form of census which he has practised on his estate in Norfolk over a period of thirty years. The procedure is to count every old and young bird seen during a series of walks over a period of about ten days. Old birds without young (commonly called "barren birds"—a misnomer, of course, since they have lost either their nests or young) and the number of old and young in each covey are all recorded separately. The results of applying this census to different estates are shown in Tables 2 and 3. On many estates I was able to do part of the counting myself in company with the keepers, and on others the counts were made by keepers and owners after the method had been explained to them. There is no reason to believe that the personal factor is a source of error in these counts, and in practice the keepers are better able to do it than anyone, since they are continually on the ground at all hours. So far as possible the same birds are not recorded twice in the same series of counts and there is usually very little risk of this being done as the coveys at that time of the year inhabit a fairly restricted area and one soon becomes familiar with their location.

Table 3. *Counts of old and young partridges made in August* 1934.

| Estate and county | Estimated total nests | Count in August | | | | Young : old ratio | % coveys surviving | Av. young per covey | Stock estimate | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Old | Young | Coveys | "Barren" | | | | Young | Total |
| L 1, Hampshire | 52 | 62 | 242 | 25 | 12 | 3·90 | 81 | 9·7 | 406 | 510 |
| C 1, Cambridgeshire | 90 | 91 | 512 | 43 | 5 | 5·64 | 94 | 12·0 | 1018 | 1198 |
| S 1, ,, | 950 | 240 | 353 | 73 | 94 | 1·48 | 61 | 4·8 | 2800 | 4700 |
| W 1, Norfolk | 150 | 161 | 444 | 59 | 43 | 2·75 | 73 | 7·5 | 829 | 1129 |
| D 2, Northamptonshire | — | 127 | 349 | 33 | 61 | 2·74 | 52 | 10·6 | — | — |
| O 1, Nottinghamshire | 525 | 169 | 593 | 61 | 47 | 3·51 | 72 | 9·7 | 4050 | 5100 |
| B 2, Yorkshire | 90 | 99 | 272 | 32 | 35 | 2·75 | 65 | 8·5 | 494 | 674 |
| S 3, ,, | 50 | 41 | 44 | 9 | 26 | 1·07 | 44 | 4·9 | 107 | 207 |
| L 2, Northumberland | 125 | 160 | 406 | 42 | 76 | 2·54 | 53 | 9·7 | 630 | 884 |
| Comparable averages: | | | | | | **2·92** | **66** | **8·6** | | |
| R 2, Hampshire | 320 | 192 | 697 | 71 | 50 | 3·64 | 74 | 9·8 | 2325 | 2965 |
| W 6, ,, | 100 | 93 | 343 | 42 | 9 | 3·69 | 90 | 8·2 | 739 | 939 |
| R 4*a*, ,, | 200 | 142 | 642 | 62 | 18 | 4·56 | 87 | 10·4 | 1830 | 2230 |
| R 4*b*, ,, | 100 | 124 | 338 | 38 | 48 | 2·73 | 61 | 8·9 | 545 | 745 |
| L 4, ,, | 70 | 91 | 395 | 40 | 11 | 4·35 | 88 | 9·9 | 609 | 749 |
| C 5, Isle of Wight | 120 | 106 | 402 | 44 | 18 | 3·80 | 83 | 9·1 | 910 | 1150 |
| P 7, Wiltshire | 53 | 56 | 148 | 20 | 16 | 2·65 | 71 | 7·4 | 278 | 384 |
| F 1, ,, | 170 | 98 | 364 | 39 | 20 | 3·71 | 80 | 9·3 | 1261 | 1601 |
| L 8, Berkshire | 180 | 156 | 427 | 51 | 54 | 2·74 | 65 | 8·4 | 1085 | 1345 |
| K 1, Hertfordshire | — | 85 | 188 | 31 | 23 | 2·21 | 73 | 6·1 | — | — |
| G 5, ,, | — | 75 | 142 | 17 | 41 | 1·90 | 45 | 8·3 | — | — |
| C 10, Suffolk | 166 | 216 | 557 | 63 | 90 | 2·58 | 58 | 8·8 | 780 | 1112 |
| H 9, Essex | — | 57 | 200 | 21 | 15 | 3·51 | 74 | 9·5 | — | — |
| W 4, Norfolk | 230 | 142 | 600 | 62 | 18 | 4·23 | 87 | 9·7 | 1940 | 2400 |
| K 2, ,, | — | 38 | 172 | 14 | 10 | 4·52 | 74 | 12·2 | — | — |
| W 11, ,, | 110 | 137 | 530 | 53 | 31 | 3·87 | 77 | 10·0 | 850 | 1070 |
| H 5, ,, | 280 | 213 | 829 | 87 | 39 | 3·89 | 82 | 9·5 | 2175 | 2735 |
| T 2, ,, | 330 | 137 | 327 | 53 | 31 | 2·40 | 77 | 6·2 | 1580 | 2240 |
| D 4, Lincolnshire | 95 | 158 | 497 | 51 | 56 | 3·15 | 65 | 9·8 | 599 | 789 |
| H 11, Worcestershire | 70 | 40 | 158 | 19 | 2 | 3·95 | 95 | 8·3 | 553 | 693 |
| H 12, ,, | 70 | 57 | 176 | 19 | 19 | 3·09 | 67 | 9·3 | 432 | 572 |
| H 10, Shropshire | — | 83 | 240 | 25 | 33 | 2·89 | 60 | 9·6 | — | — |
| H 7, ,, | 160 | 304 | 525 | 69 | 166 | 1·73 | 45 | 7·6 | 552 | 872 |
| W 7, ,, | — | 60 | 169 | 20 | 20 | 2·81 | 66 | 8·5 | — | — |
| A 2, Derbyshire | 30 | 41 | 174 | 16 | 9 | 4·25 | 78 | 10·9 | 215 | 275 |
| M 1, Northumberland | 70 | 48 | 173 | 18 | 12 | 3·60 | 75 | 9·6 | 508 | 648 |

*Note.* The records for the first 9 estates are directly comparable with those for 1933 (Table 2), in the same order.

These counts were obtained from 11 estates in 1933 and 35 estates in 1934. On 9 estates comparable counts were made in both years, and it is hoped that in future years all those counted in 1934 will be repeated and others added. Treating each estate as a sample (as with the nesting records) the averages obtained on the 9 estates with both years recorded are higher for 1933 than for 1934 which means that the chick mortality was higher in 1934 than in 1933. The most important figures in these tables are those for the ratio of young to old birds, which show the average production of young (surviving up to mid-August) per old bird. The average production per pair would of course be twice this figure. The percentage of coveys surviving is derived from the proportion of old birds seen to be without young (called "barren" birds for want of a more accurate word). It is worth noting here that Yeatter (**3**) in his study of the introduced partridge in Michigan, U.S.A., finds that not more than 50 per cent. of breeding pairs succeed in raising coveys.

In these calculations no allowance is made for mortality of adults between the nesting season and August. In 1933 and 1934 there were practically no known losses of adults at this time from disease but on estates where foxes or

cats are prevalent a few hen partridges are usually killed on the nests. The error arising from this mortality would make the figure for the production of young higher than it should be. The figures given here, however, are not much affected by this. It will be seen that in a few instances the percentage of coveys surviving is greater than the percentage known to hatch (Table 1); this discrepancy is probably due to successful second attempts at nesting after first clutches had been destroyed, the late second nests not being found for inclusion in the nesting records. The average young per covey is the number of young in coveys surviving in August.

When the total number of nests, or rather the number of *pairs* nesting, is known, a calculation of the total number of birds present in August can be made from these counts:

$$\text{Nests} \times 2 \times \text{ratio} = \text{total young.}$$

or

$$\text{Nests} \times 2 \times (\text{ratio} + 1) = \text{total population.}$$

These figures have been worked out where the necessary data are available and are given in the last two columns of Tables 2 and 3. On most estates it would be very difficult and would take a long time to make an absolute count of all the partridges in order to check these estimates, but this was done on two areas by counting in September 1934 after the crops were cut and before shooting. In Norfolk (W1) the estimated total, based on August sample counts and number of nests, was 1129, while the count in September gave 1161. For Nottinghamshire (O 1) the estimate was 5100 and the absolute count 5163.

### 4. Numbers killed.

In Table 4 the results of the two shooting seasons 1933–4 and 1934–5 are tabulated for a number of estates where records of both years are available. The number of old and young do not always agree with the total because records of old and young were made of only part of the total bag. Observation in the shooting field leads to the conclusion that the proportion of young to old killed can rarely be taken as an accurate index of the proportion actually on the ground, since, in the practice of driving, the old birds (especially those which are unaccompanied by large coveys) have a much greater chance of being killed than young ones. On the other hand, when the coveys of young birds have been split up, late in a day's intensive driving, the young birds are more likely to be killed. The discrepancy between these ratios and those obtained by counts in August cannot, therefore, be taken as indicating a high natural mortality of young between August and the shooting season. The majority of the best partridge shooting is done in October.

On 32 of the 42 estates from which the total bags are given in Table 4, many more partridges were killed in 1934 than in 1933. The gross totals for the 42 estates show a 53 per cent. increase in 1934 over 1933. This may be taken as a fair representation of the increase in numbers killed over the whole country,

Table 4. *Numbers of partridges killed in* 1933–4 *and* 1934–5 *shooting seasons. With sample records of the proportion of young to old killed.*

| Estate and county | | 1933–4 Total | Old | Young | Young: old ratio | 1934–5 Total | Old | Young | Young: old ratio |
|---|---|---|---|---|---|---|---|---|---|
| L 1, Hampshire | * | 155 | 19 | 70 | 3·7 | 240 | 46 | 138 | 3·0 |
| L 4, ,, | * | 189 | — | — | — | 524 | — | — | — |
| W 6, ,, | * | 82 | — | — | — | 65 | — | — | — |
| R 2, ,, | * | 737 | — | — | — | 1086 | 430 | 656 | 1·5 |
| L 9, ,, | | 784 | 296 | 488 | 1·7 | 1358 | 421 | 937 | 2·2 |
| M 2, ,, | * | 430 | 103 | 169 | 1·6 | 514 | — | — | — |
| C 5, Isle of Wight | * | 734 | 143 | 333 | 2·3 | 624 | 143 | 292 | 2·0 |
| F 1, Wiltshire | * | 287 | 80 | 192 | 2·4 | 354 | 100 | 227 | 2·3 |
| G 5, Hertfordshire | * | 43 | — | — | — | 97 | 17 | 33 | 1·9 |
| P 5, ,, | | 1377 | — | — | — | 1373 | 545 | 720 | 1·3 |
| K 1, ,, | * | 148 | 84 | 64 | 0·8 | 207 | 112 | 95 | 0·8 |
| C 1, Cambridgeshire | | 335 | 59 | 89 | 1·5 | 1207 | 110 | 333 | 3·0 |
| S 1, ,, | * | 1768 | 172 | 294 | 1·7 | 2398 | 893 | 1076 | 1·2 |
| H 9, Essex | * | 470 | — | — | — | 720 | 67 | 117 | 1·7 |
| C 10, Suffolk | * | 601 | — | — | — | 758 | — | — | — |
| G 6, ,, | | 1184 | — | — | — | 1702 | — | — | — |
| W 1, Norfolk | * | 145 | 44 | 101 | 2·3 | 704 | 221 | 438 | 2·0 |
| K 2, ,, | * | 90 | 22 | 48 | 2·2 | 335 | — | — | — |
| W 11, ,, | | 910 | — | — | — | 2074 | — | — | — |
| C 8, ,, | | 543 | — | — | — | 1726 | — | — | — |
| B 13, ,, | | 701 | 243 | 458 | 1·9 | 2202 | 694 | 1508 | 2·2 |
| W 14, ,, | | 741 | 141 | 126 | 0·9 | 1596 | 69 | 169 | 2·4 |
| T 2, ,, | * | 1166 | 388 | 603 | 1·6 | 2113 | 610 | 1192 | 2·0 |
| H 5, ,, | * | 1428 | 398 | 905 | — | 2545 | 662 | 1572 | — |
| H 3, ,, | | 3469 | — | — | — | 4404 | — | — | — |
| D 4, Lincolnshire | * | — | 274 | 393 | 1·4 | — | 123 | 230 | 1·9 |
| D 2, Northamptonshire | * | 581 | 95 | 110 | 1·2 | 640 | — | — | — |
| B 14, Oxfordshire | | 868 | 358 | 510 | 1·4 | 1058 | 442 | 616 | 1·4 |
| H 12 Worcestershire | * | 150 | — | — | — | 111 | — | — | — |
| H 11, ,, | * | 66 | — | — | — | 200 | — | — | — |
| D 5, Shropshire | | 56 | — | — | — | 117 | — | — | — |
| W 7, ,, | | 1100 | 358 | 742 | 2·1 | 1860 | 786 | 1074 | 1·4 |
| H 7, ,, | * | 341 | 139 | 202 | 1·4 | 550 | 262 | 288 | 1·1 |
| O 1, Nottinghamshire | * | 1786 | 279 | 642 | — | 2964 | 843 | 2121 | — |
| A 2, Derbyshire | * | 26 | — | — | — | 85 | — | — | — |
| B 2, Yorkshire | | 1011 | 95 | 273 | 2·9 | 899 | 79 | 180 | 2·3 |
| N 1, ,, | * | 206 | 80 | 126 | 1·6 | 269 | 119 | 150 | 1·3 |
| S 3, ,, | | 335 | — | — | — | 244 | — | — | — |
| H 8, Northumberland | | 484 | 137 | 271 | 2·0 | 655 | 161 | 255 | 1·7 |
| L 2, ,, | * | 321 | 60 | 150 | 2·5 | 392 | — | — | 2·2 |
| M 1, ,, | * | 311 | 98 | 193 | 2·0 | 206 | — | — | — |
| G 2, Kircudbrightshire | | 432 | 155 | 277 | 1·8 | 296 | 133 | 163 | 1·2 |
| W 10, Banff | | 869 | — | — | — | 592 | — | — | — |
| Totals | | **27460** | | | | **42004** | | | |

* The figures for these estates are directly comparable with the records of nests or counts for the same estates. On other estates the area shot over is greater than the area on which nests or birds were counted.

although only two Scottish estates are listed, both of which showed a decline in 1934. The results in the north were not so generally favourable as in the south in 1934, in fact the total of 9 estates in the north of England and Scotland is 3995 for 1933 and 3638 for 1934. It will be noted that this increase of 53 per cent. in the total number killed is more than would be expected in view of the 35 per cent. increase in nests and the lower production of young birds in 1934,

but, as already stated, the figure of 35 per cent. was probably too low, as it did not include Norfolk. If the numbers killed on 8 (one record, H 1, is missing) of the 9 estates on which this 35 per cent. increase of nests was calculated are totalled separately, they show an increase of 35 per cent. in numbers killed in 1934. Much more organised shooting took place in 1934 than in 1933 because most owners refrained from shooting many partridges in 1933 in order to preserve an adequate breeding stock.

I did not obtain very large figures to show the sex ratio of partridges killed in 1933 and 1934. The following are the results of some examinations on shooting days and of birds obtained for laboratory examination from various estates.

| | Old | | Young | |
|---|---|---|---|---|
| | Cocks | Hens | Cocks | Hens |
| 1933 | 94 | 61 | 130 | 128 |
| 1934 | 74 | 44 | 97 | 126 |

So far as possible I have avoided including the red-legged partridge (*Alectoris rufa*) in the records of nests and counts, but they are included in the total numbers killed, in Table 4, although very few are present on any of the estates listed. On two estates in Norfolk (T 2 and H 5) a fairly large proportion of red-legs were killed in 1934. On each estate 311 red-legged partridges were killed, making 15 per cent. of the bag on T 2 and 12 per cent. on H 5. This may partly account for the discrepancy between the figures for the August estimates and numbers killed on these two estates, although it is believed that the August estimates were rather below the true figure.

If the number of birds nesting in 1934 is compared with the number left for breeding (obtained by deducting the bag from the August estimates) it will be seen that a large number of birds is unaccounted for between August 1933 and May 1934. This winter "wastage" of birds from preserved estates forms one of the most important problems of game preservation and will be fully discussed in a later publication. Severtzoff (**4**), who has worked out the records of game preserved at Gatchino in Russia, found a similar high loss of partridges in the winter months; and Yeatter (**3**) records an average loss of about 5 per cent. per month in his study of the introduced Hungarian partridge in America.

Table 5. *Continuous record of* 5 *estates for* 1933 *and* 1934.

| | | 1933 | | | | | | 1934 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Winter loss | | | | | |
| Estate and county | Acreage | Nests | August estimate | Number killed | Number left | Birds | % | Nests | August estimate | Number killed | Number left |
| L 1, Hampshire | 1100 | 40 | 455 | 155 | 300 | 196 | 65 | 52 | 510 | 240 | 270 |
| S 1, Cambridgeshire | 11000 | 650 | 3930 | 1768 | 2162 | 262 | 12 | 950 | 4700 | 2398 | 2402 |
| W 1, Norfolk | 1400 | * | 712 | 145 | 567 | 267 | 47 | 150 | 1129 | 704 | 425 |
| O 1, Nottinghamshire | 5000 | 471 | 4522 | 1786 | 2736 | 1686 | 62 | 525 | 5100 | 2964 | 2136 |
| L 2, Northumberland | 2000 | 100 | 1187 | 321 | 866 | 616 | 71 | 125 | 884 | 392 | 492 |

* Number of nests not known accurately. 712 partridges were counted on the ground in September 1933.

In Table 5 the records are summarised for five estates on which complete data are available for 1933 and 1934. S 1, Cambridgeshire, is the only one of these which shows a reasonable figure for number of nests in 1934 compared with the stock left over from 1933, but on the other four the stock left was considerably in excess of that required to give say 50 per cent. increase of nests in 1934. The stock left on these four for 1935 is rather less than was left for 1933, so it will be interesting to see the number of nests in 1935 and whether a similar high winter wastage takes place.

## 5. SUMMARY.

A system of recording the numbers of partridges (*Perdix perdix*) has been developed and applied to a number of estates in England and the population statistics obtained during the years 1933 and 1934 are tabulated. After two years of disease and low numbers in 1931 and 1932 there was an increase in numbers in 1933 and 1934. The number of breeding birds was more than 35 per cent. greater in 1934 than in 1933. Sample censuses in different parts of England were carried out in the summer, on 11 estates in 1933 and 35 estates in 1934, which show that the numbers of young reared per pair was slightly less in 1934 than in 1933. 53 per cent. more partridges were killed in 1934 than in 1933, taking the gross totals of 42 estates.

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# NOTES

## INTRODUCTION OF GREEN LIZARDS INTO WALES.

THREE and a half years ago 20 green lizards of the species *Lacerta viridis*, purchased from a London dealer, were liberated on the rocky coast of Portmerion, the property of Clough Williams-Ellis, Esq., in the county of Caernarvonshire, North Wales. The animals have been repeatedly seen in the intervening period, but their present number is unknown, and as yet there is no evidence that they have bred.

S. ZUCKERMAN.

## SOME ESCAPES OF COYPUS (*MYOPOTAMUS COYPU*) FROM NUTRIA FARMS IN GREAT BRITAIN.

DURING the last few years several coypus escaped from nutria farms have been killed in various parts of Britain. One was shot on May 11th, 1932, at Warnham Mill Pond, Warnham Court, Horsham, Sussex. It weighed 11 lb. 2 oz. and had a total length of 35 in. It was the only specimen obtained in this district and its source is unknown. The skin and skull were examined by the Bureau of Animal Population. Another adult coypu was killed at Worlington, near Mildenhall, West Suffolk, in September or October 1933. It was shot in a small brook which flows into the River Lark and had escaped from a local fur farm. A coypu was shot on September 19th, 1934, at the farm dam, Clackmarras Farm, Longmorn, Elginshire. The total length was 31 in. and the weight 11½ lb. The animal was said to have taken up its quarters in a field, and had been seen several times going to and from the farm dam. When intercepted by a terrier it severely injured the dog and escaped. On November 13th, 1934, one (also apparently full grown, about 30 in. in total length) was shot at Cabrach Lodge, Cabrach, Banffshire. This animal had been seen on previous occasions by the keeper who shot it. It seems to have been living in a marsh connected with the burn where it was shot. A field investigator who examined the locality soon after the shooting of the animal, found footprints on the banks of the River Deveron, near by, which he thought might be those of young coypu. In this case another adult may well be still at large here. Both the above animals may have come from a fur farm at Rothes on the River Spey, Elginshire, from which three coypus are said to have escaped in the late summer of 1934. Longmorn is about 7 miles from Rothes; to reach it the animal would have to pass through the narrow Glen of Rothes. Cabrach is about 37 miles upstream from Rothes along the River Isla and towards the headwaters of the River Deveron, it lies above the 1000 ft. contour. Coypus had been taken in the open outside Scottish nutria farms before this.

In its native home in South America the coypu ranges from the semi-tropical zone to the colder south. Ice does not inconvenience it. It is often active in daylight.

It is interesting to compare the potentialities of the coypu as a pest with those of the muskrat. Almost anywhere in Great Britain, with its temperate climate, the coypu could readily find a quiet stream, marsh or pond suitable to its aquatic habits. So far as is known it has not established itself in the wild state. Its breeding rate is not as great as that of the muskrat, neither is it so elusive, or so truly aquatic in its habits. Its large size, excursions on land, partly diurnal habits, and a certain lack of wiliness, make it easy to see and kill. Taking these points into consideration, it does not seem as though the coypu would readily establish itself in the first place, and its extermination, if necessary, should not be difficult. The coypu might be able to damage embankments; but the burrow does not invariably open under the water. The burrowing habits of the coypu are not really well developed. In France and Germany, where there are many nutria farms, there is no evidence of damage arising from their spread in the wild state.

I am indebted to the Ministry of Agriculture and Fisheries for the data on the coypu at Worlington, and to the Department of Agriculture for Scotland for details about the Scottish records.

TOM WARWICK.

Since the above was written information has been received that a coypu was seen on April 29th, 1935, in a pond at Ends Place, Warnham, Sussex. This is close to Warnham Mill pond, where one was killed in May 1932.

# REVIEWS

## THE FEBRUARY ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. XXIII, NO. 1).

This issue contains nine original papers, two reviews and the annual account of the proceedings of the British Ecological Society with the Society's accounts and list of members. There are three long and important ecological studies: Mr R. E. Moreau's synecological study of the Usambara Mountains in the north of Tanganyika Territory, in which he gives an excellent description of the different types of forest in this region, especially as habitats for birds; Mr Kenneth Rees' thorough account of the marine algal vegetation of Lough Ine in the south of Ireland with much new information on the factors determining the various communities; and the second part of Mr N. V. Polunin's paper on the vegetation of Akpatok Island, Hudson Strait, with a very clear and useful summary of the different habitats, communities and successions he was able to trace. Shorter papers are Prof. R. S. Adamson's six years' study of regeneration after burning on Table Mountain, Cape Colony, in which he shows that the previously dominant sclerophyll shrubs re-establish themselves during that time, but in less numbers, partly by shooting from the stools and partly from seed, while the proportions of the different life-forms present undergo significant changes; the two concluding sketches of Prof. William Seifriz's attractive series on the vegetation of southern Russian provinces, illustrated, as before, by beautiful photographs; and a description by Mr Wyllie Fenton of the production of grassland from woodland and moorland in various parts of Scotland. Prof. P. A. Buxton contributes some interesting photographs of seasonal changes in the vegetation of northern Nigeria with valuable meteorological data; and finally Prof. John Phillips publishes the second part of his very fully documented account of the "organismal" concept of vegetation and its development.

Dr A. R. Clapham contributes an interesting critical review of the new English edition of Raunkiaer's works and Mr Charles Elton reviews the November 1934 issue of the *Journal of Animal Ecology*. The number concludes with a notice of the very successful summer meeting of the Society at Bangor, North Wales, and of the soirée and annual meeting at University College, London.

A. G. TANSLEY.

## "EPPUR SI MUOVE."

(1) **Alfred J. Lotka.** *Théorie analytique des associations biologiques.* Part 1: *Principes.* Actualités Scientifiques et Industrielles. 187: Exposés de Biométrie et de Statistique Biologique. 1934, pp. 1–45. (Hermann et Cie, 6 Rue de la Sorbonne, Paris 6.)

(2) **S. A. Severtzoff.** *On the dynamics of populations of vertebrates.* Q. Rev. Biol. 9, 409–37. 1934. Baltimore.

(1) When Lotka published his first notes on this subject in 1920, animal ecology had entered on a new phase, though we are probably only now beginning to see the importance of it. There were not at that time statistics for wild animal populations with which his theories could be put to the test. Since then a small constellation of workers has grown up – one cannot call it a group, since most of its members live in different countries and often question the validity of each other's conclusions. It includes Alfred J. Lotka, an American university mathematician; two Italians, Vito Volterra and Umberto d'Ancona, one a professor of

mathematics and the other a fishery research worker; two Australians, A. J. Nicholson, a Federal economic entomologist, and V. A. Bailey, another professor of mathematics; the British parasite-entomologist W. R. Thompson; and a Russian, S. A. Severtzoff, working on game research. This scattered distribution in five countries of people working from half-a-dozen angles is typical of pioneer work in any new branch of ecology, but the results bear the stamp of independent lines of thought converging upon a common problem. This problem is the central one of animal ecology: the organisation and dynamics of animal populations. It lies at the root of most thorny problems in economic biology—epidemics and pests (whether insect or bird or mammal) on the one hand, and the fisheries and whaleries, fur trade, game management and conservation on the other. Ecologists are beginning to give full attention to the collection of adequate population figures for wild animals and to the study of animal communities as a whole. Administration and big business are beginning to find it difficult to ignore the usefulness of such studies, while zoologists (especially geneticists) are realising the need for reliable information about the "struggle for existence" among wild species. Behind these ordinary ecological investigations, concerned with organisation of observers, census techniques, and all the paraphernalia of field surveys and the laboratory and museum activities that go with them, lies this basic work upon populations treated by Lotka. He seeks to create a system of mathematical formulae which will guide the ecologist in his population studies. But realising that the success of mathematics in biology depends on the assumptions upon which they are based, Lotka tackles some preliminary matters. He sees population studies as an attempt to calculate the distribution and redistribution of a certain amount of available matter among a complex series of living organisms. In doing this we ought to be able to use the type of mathematical equations already worked out for chemical changes. His "équation de liaison", of which $2H_2+O_2=2H_2O$ is an example, has its ecological parallel in a food-cycle diagram. In calculating *how* such changes occur, as distinct from showing that they *do* occur, it is necessary to use concepts of probability and frequency. Lotka points out that the chief difference here between physico-chemical and biological systems is that the units whose probable quantities are being studied are invisible in the former, but visible in the latter. This is a practical rather than a fundamental difference. Here the author discusses at some length the concept of "time" in biology, especially in its relation to the laws of thermodynamics. This discussion is interesting, but its exact relation to the theme will be looked for in future instalments of his work. He next points out that evolution and population changes may be defined as the redistribution of matter and energy by means of the powers of selection and concentration of the organism, resulting in progressively greater control over the environment. There is an amusing remark about technical terms: "Nervous energy, vital force, entelechies, *et hoc genus omne*,—names that wander about the world seeking a subject to which to attach themselves. Science does not advance in this way. It must find the subject and prove the necessity of giving a name, before celebrating the baptism." After this preamble Lotka begins his detailed attack on the problem. Like most mathematicians, he takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown. Hence the reviewer's difficulty in criticising the mathematical section. Although the whole animal community is the ultimate object of study, a simple case of two species is treated first. Hardy's herring and plankton food-cycle diagram is reproduced to show the necessity of simplifying the issue. The upshot of several pages of mathematical discussion—the condensation and extension of previous studies—is that we get various formulae for the conditions controlling the growth of populations. The importance of the method is this: if we know certain variables, mostly desired by ecologists and in some cases already determined by them, we can predict certain results which would *not* normally be predictable or even expected by ecologists. The stage of verification of these mathematical predictions has hardly begun: but their importance cannot be under-estimated, and we look forward to seeing the further volumes of Lotka's studies.

(2) Severtzoff, who has carried out some important surveys of game-animals and birds in Russia and Siberia (including the mapping of a hare pandemic extending over 2000

miles of country), attempts to combine in one study the creation of mathematical expressions for animal populations and the demonstration of their truth by field statistics. His formulae require as a first basis knowledge of all such factors as number of young, age of sexual maturity, frequency of litters, gestation periods, sex-ratios, number of non-breeders, and so on. Much harder to obtain are figures for mortality at different ages and in different years. But the first set of variables gives an expression for the potential rate of population increase (Chapman called it *biotic potential*, Severtzoff calls it *potential of fertility*). The difference between this and any actual census figures should throw light on the mortality incidence. This he attempts to check in a very interesting analysis of game records kept on the Imperial Russian hunting estate at Gatchino, near Leningrad, between the years 1886 and 1909. Here the capercaillies, black-grouse, heath-cocks, ptarmigan, partridges and pheasants, were very carefully preserved and game bags recorded. Partridge numbers are analysed, but the data for different fertility factors are insufficient for refined analysis. There was a well-marked periodicity in numbers, and the chief mathematical conclusion of value is that the increase phase of each cycle gives a straight line if the figures are plotted logarithmically (the same is true for some Canadian lynx figures), and that the angle of this line is characteristic for each cycle. The testing of formulae for increase is carried further for a herd of roedeer (introduced into the park and increasing under protection). Here the author obtains quite a good fit between theory and result, except in later years when he is forced to assume mortality in the deer. Other matters are also discussed, in particular the validity of certain conclusions of Volterra's, with which Severtzoff agrees. It is at any rate clear that ecologists have much to gain by systematising their methods and by using mathematical techniques, while on the other hand the perfection of the latter awaits the result of complete population studies in which fertility rates are combined with census work and an adequate field and laboratory organisation for measuring and finding the causes of mortality. Severtzoff's study would have been of even greater value if he had given more details about his methods and about the methods of game management used on the Gatchino estate.

CHARLES ELTON.

## PARTRIDGES IN AMERICA.

**Ralph E. Yeatter.** *The Hungarian partridge in the Great Lakes Region.* University of Michigan School of Forestry and Conservation Bull. No. 5. 1935. 92 pp. illustrated with maps and photographs. (University of Michigan Press, Ann Arbor, U.S.A. Price 35 cents.)

THE partridge (*Perdix perdix*), one of the commonest game birds of Europe, has been introduced into the United States in order to augment the native game birds. This is the first publication which gives a clear picture of the life of the partridge in America. It is surprising to know that approximately 260,000 European partridges were released in the United States and Canada between 1900 and 1933. The work of Yeatter has been concentrated in Michigan over a period of three years, 1929–32, but he has obtained information about partridges in other States as well. An intensive population study was made on a definite area of about 1800 acres, where as far as possible everything that happened to the birds was recorded.

Most of the data were obtained by field observation, but no large number of birds was examined *post mortem*, so that evidence on parasites and food is not so complete as it might be. Seeds and leaves form much the greater part of the food of adults while the young eat more animal food (chiefly insects). Disease was rare during the period of observation, but three cases of avian tuberculosis were encountered. 76 partridges were examined for parasites but only two species of worms were found (*Heterakis* sp. and *Dispharynx spiralis*). No specimens of the nematode *Trichostrongylus tenuis* were found: this is a very common parasite of partridges in England and is known among bobwhite quail and other birds in America. The natural increase and mortality was traced by census counts on a selected area, where no shooting for sport took place. There was an overall increase from 113 in January 1931 to 267 in January

1933 on the 1800 acres. Losses of nests and mortality among chicks were the most serious checks to rapid increase. Over half the breeding birds failed to raise broods and there was a loss between hatching and maturity of about 4 young per brood. Late autumn and winter mortality was at a fairly uniform rate of about 5 per cent. per month. The question of movement of adults away from their home area at the pairing time does not seem to have been considered, all winter and early spring losses being counted as mortality. But movement *must* take place or the partridge would not extend its range? It is evident that the small relative increases shown in these years (which were considered favourable seasons) leaves little margin for shooting. If partridges are treated as a crop for sportsmen (as in England) it is obvious that the Americans must make definite efforts to lessen the natural mortality—particularly that due to farming operations in the nesting season. The remarks on management with this object deserve the closest attention by all who wish to increase their stock of partridges.

A. D. MIDDLETON.

## THE SURVEY OF PLANT COMMUNITIES.

**R. Bracher.** *Field studies in ecology.* 1935, 100 pp. (Bristol and London, J. W. Arrowsmith Ltd. Price 2*s.* 6*d.*)

THE animal ecologist is now well equipped with text-books upon plant ecology. We have Tansley's *Practical plant ecology* (1923), Tansley and Chipp's *Aims and methods in the study of vegetation* (1926), Johnstone's *Plant ecology* (1928), Anderson's *Natural woodlands of Britain and Ireland* (1932) (also the rather more general and elementary, and less satisfactory, *Plant and animal ecology*, by Stork and Renouf). The present book is well arranged, clearly written, and cheap. It combines in a short space (for the 100 pages are small ones) the main classification of plant associations (dealt with in detail by Johnstone, by Anderson, and by Tansley in the now out-of-print *Types of British Vegetation*), together with a well-balanced introduction to field methods for making quadrats and recording environmental changes by means of instruments. The methods are of course dealt with more fully in *Practical plant ecology*, but the latter lacks the description of plant associations, illustrated by lists from actual places, which are an attractive feature of the present book. It should be found convenient and useful to both schools and university students, as well as to animal ecologists who have not already been trained in the subject. One misses any references to Johnstone's or Anderson's books, while the tremendous influence of grazing and seed destruction by animals are perhaps not sufficiently emphasised.

CHARLES ELTON.

**Irvine Whittaker.** *Birds of a Lancashire cotton town, being notes on the Avifauna of Heywood.* 159 pp. Photos and a map. Heywood, Lancs. 1935 (2nd ed.).

THE borough of Heywood includes an area of 13 square miles. The town itself is in the valley of the polluted river Roch, at an altitude of 400 ft. and has a population of 25,000, but within the area of the borough is a moorland region rising to Knowl Hill, 1378 ft., an outlier of the Pennines. From this high ground brooks descend to the river in cloughs, which are fringed with hanging woods in their lower portions. Apart from the characteristic birds of the moorlands—red grouse, curlew, dunlin, golden plover, merlin, twite, ring ouzel—and the streams—dipper, grey wagtail, sandpiper—the chief feature of ornithological interest is the sewage farm. The sprinklers and the rank growths of weeds attract flocks of finches and pipits in winter, and many wagtails, swallows and swifts on migration. The author states that swifts are sometimes so numerous there that the workmen have difficulty in performing their

duties. One is led to wonder whether the provision of such a rich feeding ground for the birds may not even have compensated for the reduction of their feeding grounds elsewhere due to the spread of the town.

Most of the foregoing facts are taken from the preface which we think might well have been longer and given more particulars of the species found in each type of habitat described and their relative numbers. In the annotated list which comprises the bulk of the work there are many facts of interest which might usefully have been brought together in the preface. We are told for instance that there is no game preserving in the district and that as a result the birds of prey suffer no persistent suppression. On looking up the author's remarks on those species which in other parts of England are destroyed in such numbers by keepers we find that the carrion crow and the jay are unknown at Heywood, the sparrowhawk is scarce and decreasing, two, and occasionally three, pairs of merlins breed on the higher moors, whilst magpies are abundant. On the other hand grouse are common on the moors and partridges in the fields. The keeperless borough of Heywood would appear therefore to show the same relation between the numbers of these species as is found on many well-keepered estates.

Among many other points of interest we note that the corncrake continued to be a common nesting species in the district until about 1915, though for a few years prior to that time its numbers had shown a tendency to decline. In 1915 at least ten pairs nested in the district, but in 1916 the author only heard a single bird during the whole season and since then only one or two pairs have nested each year. Such a sudden decrease can hardly be attributed solely to the introduction of machine-mowing in place of hand-mowing, which is the cause most frequently suggested to account for the change, though the author notes that the two changes coincided in the district.

W. B. ALEXANDER.

## HERRINGS AND ALGAL SLIME.

**R. E. Savage** and **A. C. Hardy**. *Phytoplankton and the herring.* Part 1: 1921 *to* 1932. Ministry of Agriculture and Fisheries, Fishery Investigations. Ser. 2, 14, no. 2, pp. 1–73, 1935. (London, H.M. Stationery Office, Price 3*s.* 6*d.* net, postage extra.)

As herrings live on plankton animals that in turn depend on phytoplankton for food, it was hardly to be expected that systematic phytoplankton surveys in the North Sea would show that herrings *avoid* some of the densest patches, especially of the diatoms *Rhizosolenia styliformis* and the colonial flagellate *Phaeocystis*. Yet this conclusion appears to be inescapable in face of the evidence brought forward in this report. Scoresby (1820) noted the dense patches of diatoms and *Phaeocystis* that discoloured the sea, and Brown found out what they were in 1866. In 1884 Pearcey described the slimy diatom patches which coated the nets of herring fishermen near the Shetlands, and noted the general absence of fish from such waters. Bullen in 1906 and 1907 found a similar relation between "stinking water" due to excess phytoplankton, and the success or otherwise of the autumn herring fishing in different years.

Hardy's plankton recorders were used to obtain some of the data in the present survey. The patches of *Phaeocystis* or diatoms may stretch for fifty or a hundred miles. Although it is not yet known for certain whether these patches actually prevent migration of herring shoals, it is at any rate clear that the fish avoid the patches. "When the fish have been plentiful and the fishing above the average we find no instance of concentration of phytoplankton in such a position where it might be held to have an influence on the fishery. On each occasion when the fishing has been below the average, and this decrease cannot be attributed to interference by stormy weather or economic conditions, we can point to phytoplankton concentrations as being possible important contributory factors." This study covers a wide field of ecological facts, and was made possible by a background of surveys

carried out steadily and over a number of years by the various fishery stations on the East Coast, especially the Government station at Lowestoft, and the more recent Department of Zoology and Oceanography at Hull University. It is of some significance that the phenomenon was well known to North Sea fishermen long before it received scientific study. They refer to the unwelcome patches of algae variously as "weedy water", "stinking water", or "Dutchman's baccy juice".

CHARLES ELTON.

## THE MENTAL PATTERNS OF BIRDS.

**Eliot Howard.** *The nature of a bird's world.* 102 pp. (Cambridge University Press, 1935. Price 7*s.* 6*d.*)

Among the privileges of a distinguished naturalist is that of writing discursive books in order to clear his own mind on matters of theory. We have already seen this method employed by H. G. Wells (a human ecologist), and now Eliot Howard has employed it in order to introduce the reader to the very complicated subject of bird life and bird mind. The method justifies itself, in so far as any cut-and-dried system of simple formulae would give an entirely untrue impression of the present state of the science of bird psychology. We are all the time conscious while reading this book that it is written by the man who first described in detail the territory systems of warblers, following this study up with other important territory observations. An attempt is made throughout to describe behaviour objectively, to weigh the validity of all the technical terms employed, and to draw limited conclusions which are trustworthy rather than make sweeping generalisations. The examples denote a brilliant field observer. Certain phenomena stand out clearly: the reproductive behaviour of birds follows a definite sequence which the author believes will in a large degree be explained by a definite physiological sequence working in conjunction with spring weather conditions; the inter-relations of the various parts of this pattern of behaviour are difficult to describe in detail, but they show every sign of being a connected whole. Under certain conditions bits of behaviour will suddenly appear in an unexpected context, as when a moorhen drives out a strange female from his territory, but stops to mate with her before again attacking ferociously. One is irritated, however, by the concentration of discussion upon the sexual side of the bird's life. Irritated, not by the obviously mechanised reactions which characterise this phase of bird behaviour (they are found also in the monkeys studied by Zuckerman and probably also in man), but by the argument from these conclusions on sexual behaviour to general conclusions about the bird mind. It would seem fairly likely that the reproductive and digestive functions of a bird or mammal's life are far more closely under the control of glands which influence the nervous system than under the direct control of the brain. Although, again, it is futile to try and decide now whether the brain actually determines every phase of the mind's activities, it is at least likely that brain decisions work on a very different plan to "gland decisions". What are needed in animal ecology, and needed urgently, are empirical experimental studies of the nature of animal choice in circumstances not directly concerned with mating, e.g. choice of habitat. In other words a knowledge of the simple physiological nature of actions which are controlled by a lower bodily hierarchy (such as the sex glands) does not necessarily help us to understand the nature of choice by the brain itself. This distinction incidentally may explain a good deal of the ordinary person's antagonism to some of the conclusions of modern experimental psychology.

CHARLES ELTON.

# NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

The entomological journals have been abstracted by H. F. Barnes, John Ford and B. M. Hobby; the others by D. H. S. Davis, Charles Elton and A. D. Middleton.

This series of notices covers most of the significant work dealing with animal ecology published in British journals, large and small. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, University Museum, Oxford.

Copies of these abstracts, cut down to a width suitable for pasting on to five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 200 notices, in two sets, May and November).

## 1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

**1. Witherby, H. F. (1934).** "The names of the song-thrushes." British Birds, 28, 186–7.

*Turdus philomelus philomelus* has been changed to *T. ericetorum philomelus* owing to the unfortunate discovery of a prior naming in 1807. It is pointed out in defence of the change that only about one change of this sort has been made each year in British Birds names during the last ten years.

**2. Frohawk, F. W. (1934).** "The complete book of British butterflies." 384 pp. Many coloured and text illustrations. (London and Melbourne, Ward, Lock and Co. 10*s*. 6*d*.)

**3. Killington, F. J. (1934).** "On the life-histories of some British Hemerobiidae (Neur.)." Trans. Soc. British Ent. 1, 119–34.

Accounts of the distribution, habitat and life history of four species of brown lacewings, with descriptions and figures of the earlier stages.

**4. Lal, K. B. (1934).** "The biology of Scottish Psyllidae." Trans. R. Ent. Soc. Lond. 82, 363–85.

Detailed accounts of ten species of "jumping plant-lice" occurring on alder, ash, box, hawthorn, pear, willow, nettle and willowherb. Includes life history, observations on the effect of the larvae on the host plants, and descriptions of the adults and of their seasonal colour phases.

**5. Audcent, H. (1934).** "British Liriopeidae (Diptera, Nematocera)." Trans. Soc. British Ent. 1, 103–18.

Describes the structure and life history of a typical representative of the family (formerly known as Ptychopteridae, and related to crane-flies); gives a key and descriptions of the seven British species.

**6. Rolfe, S. W. (1934).** "Notes on Diplopoda. 1: The re-study of a widely distributed British millipede, *Ophyiulus pilosus*, Newport." Ann. and Mag. Nat. Hist. 14, 192–203.

Full description of the structure.

## 2. ECOLOGICAL SURVEYS AND HABITAT GROUPS.

### (*a*) Marine.

See also **12, 33.**

**7. O'Mahoney, E. (1933).** "Notes on the fishes of the North Bull area, Dublin Bay." Irish Nat. J. 4, 179–80, 203–5, 223.

List of species in a tidal creek.

(*b*) Freshwater.

See also **21, 33, 76, 85.**

**8. Britten, H.** and **Williams, E. G. (1934).** "Notes on the survey of the natural history of a small area." N. Western Nat. 9: 19–21, 127–35.

List of animals (all vertebrate groups, also Mollusca, Rotifera, Polyzoa, beetles (Coleoptera)) and phytoplankton, from a pond on the Cheshire grasslands. The vertebrate fauna comprised: vole (*Microtus*), reed bunting, mallard, heron, snipe, moor-hen, coot, frog, common toad, crested newt, and ten-spined stickleback.

**9. Oldham, C. (1933).** "Note on the palmated newt." Trans. Hertfordshire Nat. Hist. Soc. and Field Club, 19, 209–10.

Draws attention to need for exact records of the distribution of *Molge palmata*. Its range overlaps much of the ranges of the common and crested newts. It is absent from Ireland, Shetland, Orkney, Isle of Man, Outer Hebrides, but occurs on Anglesey, Bardsey, Isle of Wight, Channel Is., and Sanda, off the Mull of Kintyre.

**10. Walton, C. L. (1933).** "Fresh-water Gastropoda from Skokholm Island." N. Western Nat. 8, 326.

Five species including *Limnaea truncatula*: there is, however, no liver fluke disease either in sheep or rabbits there.

**11. Elmhirst, R. (1935).** "The occurrence of *Gammarus* in Scottish waters." Scottish Nat. 17–21.

A study, partly experimental, of the four species of *Gammarus* found in the Clyde area (the marine *G. locusta*, and *G. marinus*, the estuarine and brackish *G. duebeni*, and the freshwater *G. pulex*). Experiments in gradients of salinity showed that *G. locusta* and *marinus* did not attempt to enter fresher waters, but that *G. duebeni* had a decided tendency to do so. Certain freshwater *Gammarus* populations in the district, also in the Isle of Man, approach *G. duebeni* in structure. It is not known whether these are *pulex* or *duebeni*, or hybrids.

(*c*) Land.

See also **3, 4, 49, 54.**

**12. Peacock, A. D., Smith, E. P.** and **Davidson, C. F. (1934** and **1935).** "The natural history of South Rona." Scottish Nat. 1934, 113–27, 149–63; 1935, 3–10.

An expedition from St Andrews University made surveys in July 1933 on this island, which is near Skye, and is about five miles long. The population had fallen from 160 to 3 in the last fifty years. The results of surveys include physiography, geology, vegetation and zoology. In caves and kitchen middens were found bones of ox, sheep, and seal, and remains of edible molluscs (*Mytilus, Ostrea, Patella,* and *Littorina*). Lists are given of marine Mollusca from intertidal silt and rocks, and from tow-netting in the Laminarian zone; also lists of beetles, sawflies, flies and spiders, which include some habitat notes. There is a complete vegetation survey. Trapping for rodents, and fishing, were unsuccessful.

**13. Serle, W. (1934).** "Note on the breeding birds of the island of Hoy, Orkney." Scottish Nat. 129–36.

A list, together with notes on habitats and abundance. The Great Skua (*Stercorarius skua*) breeds regularly. Records peregrine falcon eating arctic tern and puffin.

**14. Temperley, G. W. (1934).** "The British willow-tit." Vasculum, 20, 134–7.

Nesting habits and distribution.

**15. Wynn-Williams, M. (1934).** "Some insect and fungoid pests of *Carduus* and *Cnicus* species." N. Western Nat. 9, 24–30.

A detailed account of fungi and insects of thistles. The insects include froghopper, Capsid bug, earwigs, Thysanoptera, an Aleyrodid, Aphids, various unidentified larvae, midges (attacking the seeds), weevils, mangold fly and celery fly. Also slugs.

**16. Burr, M. (1935).** "British Orthoptera." Ent. Rec. 47, 8–9.

Appeals for information on the following points: (1) Status of the field-cricket in Britain. (2) Where do the mole- and wood-crickets occur outside Hampshire? (3) Do the genuine *Acrydium bipunctatum* and (4) *Staurodcrus vagans* occur here? (5) Does *Phaneroptera falcata* really occur in Cornwall? (6) Northerly range of British Delticids. (7) Orthoptera of Ireland, Wales and Scotland. (8) Does *Apterygida* occur away from hop gardens? (9) Is *Labidura riparia* confined to Boscombe? Replies should be sent to United University Club, Pall Mall East, S.W. 1.

**17. Laidlaw, W. B. R. (1934).** "Notes and observations on the conifer root aphis *Pachypapella piceae*, Htg. (*Pemphigius piceae*, Tullgren)." Scottish Forestry J. 48, 79–84.

The larvae of this Aphid live in colonies of soil in pockets in the soil round the secondary rootlets of pine and spruce seedlings. They secrete a waxy substance that lines the pocket and covers the root tips. Description and life history.

**18. Omer-Cooper, J.** and **Tottenham, C. E. (1934).** "Coleoptera taken in the air at Wicken Fen." Ent. Mon. Mag. 70, 231–4.

By sweeping the air for six hours, over 7000 beetles were captured. 60 per cent. of these individuals belonged to species new to the Wicken list. The total number of species was 81, twenty-five species were not in the Wicken list and the majority of the remainder had been previously recorded by one or two workers only. This rather novel site for sweeping reveals a difficulty in assessing insect populations.

**19. Curtis, W. P. (1934).** "A list of the Lepidoptera of Dorset. Introduction and Part I." Trans. Soc. British Ent. 1, 185–286.

A comprehensive list, with notes on distribution, habitats, frequency of occurrence and variation of Artiadae, Nolidae, Hylophilidae, Caradrinidae and Plusiadae.

**20. Davies, W. Maldwyn (1934).** "The Collembola of North Wales. Zone 1: Mountain (*a*) Soil fauna." N. Western Nat. 9, 115–24.

Detailed lists and localities of 30 species (including 6 new to Britain), without any general conclusions about distribution.

**21. Davies, W. Maldwyn (1933).** "*Culex pipiens* L. in caves." N. Western Nat. 8, 325.

Abundant in Cefn Caves, North Wales, in November. Also spiders (*Meta menardi*) and a few Collembola.

**22. Bristowe, W. S. (1935).** "Spiders from the Isle of May." Scottish Nat. 27–8.

Records 17 species of spiders and two harvest spiders from this island in the Firth of Forth. One of the latter, *Nelima silvatica*, is only known elsewhere in Britain from Skokholm, Pembrokeshire. It shows certain differences in both places from the continental form, suggesting that the species is a formerly widespread one now restricted to the two islands.

### 3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **11**, **47**.

**23. Bateman, J. B. (1935).** "Mitogenetic radiation." Biol. Rev. 10, 42–71.

There is now a large literature on the subject of possible short-wave radiation from living matter, affecting other living matter or physical instruments. There are positive and negative records, and there is not sufficient confirmation of the positive records to prove the hypothesis. It is probable at any rate that the "radiation" has nothing to do with ultra-violet radiation.

**24. Jourdain, F. C. R. (1934).** "Song-thrush attacking lizard." British Birds, 28, 112.

Attacked *Lacerta vivipara*, which shed its tail. The thrush managed to swallow the tail, and the lizard escaped.

**25. Boyd, A. W. (1934).** "Black-headed gulls nesting in trees." British Birds, 28, 115–17.

A very unusual site for this species, noted on a Cheshire mere.

**26. Oldham, C. (1934).** "Retarded development in the frog (*Rana temporaria*)." Trans. Hertfordshire Nat. Hist. Soc. and Field Club, 19, 211–12.

Records an instance of frog tadpoles surviving winter out of doors and metamorphosing the following spring.

**27. Evans, A. C. (1934).** "Studies on the influence of the environment on the sheep blowfly, *Lucilia sericata* Meig. 1: The influence of humidity and temperature on the egg." Parasitology, 26, 366–77.

Loss of water by the egg is held to be the cause of death at certain temperatures and humidities.

**28. Green, E. E. (1934).** "Moths attracted by the blossoms of *Andromeda floribunda*." Entomologist, 67, 147.

The blossom of this bush, although possessing no appreciable scent, is recorded as remarkably attractive to moths.

**29. Mellanby, K. (1934).** "Effects of temperature and humidity on the clothes moth larva, *Tineola biselliella* Hum. (Lepidoptera)." Ann. Appl. Biol. 21, 476–82.

The larvae dry up when kept in dry air. A considerable amount of dry matter is lost by excretion and the production of silk. These factors were estimated quantitatively by experiments.

See also paper by same author: "The site of water loss from insects", Proc. Roy. Soc. B, 116, 139–49, dealing with the same subject. It is shown that increase in $CO_2$ or decrease in oxygen content of air makes the spiracles open, and remain open, with rapid loss of water.

**30. Nixon, G. E. J. (1934).** "Notes on Wasps. III." Ent. Mon. Mag. 70, 265–70.

The vigour of a failing nest of *Vespa germanica* was restored by introducing callow workers of *Vespa vulgaris*.

**31. Spooner, G. M. (1934).** "Ejected Dipterous prey of *Metacrabro quadricinctus* F. (Hym., Crabronidae)." J. Soc. British Ent. 1, 48–53.

A small colony of this wasp had burrowed in an oak tree. Prey already stored was repeatedly dragged to the mouths of the burrows and ejected, while other members of the colony were still bringing in and storing fresh prey. The ejected prey was not stored again, although in good condition. The author suggests that there was exceptional congestion in this particular nesting site and that, in extending the burrows, the wasps tunnelled into cells already stocked. A list of 259 specimens of 42 species of prey is given. All are Diptera, the Anthomyiidae and Tachinidae predominating and males exceeding females in a proportion of 2 : 1.

**32. Edwards, F. W. (1934).** "*Microsania pectinipennis* Mg. (Dipt., Platypezidae) attracted to bonfire-smoke." J. Soc. British Ent. 1, 31–2.

This fly, formerly believed to be rare, is attracted in large numbers to heath fires. The males swarm in the smoke, but the females keep low over the smouldering embers where they may be seen to settle. Experiments suggest that this species is specially adapted to resist noxious fumes or oxygen deficiency. The life history is unknown, but a clue may be provided by the nymphal mites (*Parasitus*) with which the flies are heavily infested. Many species of this genus of mites are found on fungi where they prey on other Acarines.

**33. Morton, K. J. (1934).** "Habits of the larvae of Hydoptilidae (Trichoptera)." J. Soc. British Ent. 1, 44–5.

Discusses the web-spinning habits of the larvae of this family of caddis-flies. Records that the Gulf of Finland supports a rich fauna of larval Trichoptera owing to the comparatively low salinity of the water. States that many Trichoptera were once found at rock pools on the Scottish coast and that the dragon-fly *Sympetrum striolatum* was suspected to breed there.

**34. Parkin, E. A. (1934).** "Observations on the biology of the *Lyctus* powder-post beetles, with special reference to oviposition and the egg." Ann. Appl. Biol. 21, 495–518.

This work shows that Fisher and Clarke's theory regarding the relationship between the wood vessel diameter and liability to attack must be restated in order to make it clear that the liability of a timber to *Lyctus* attack depends on the relationship between the vessel diameter of the timber and the ovipositor diameter of the beetle.

**35. Hora, A. M. (1934).** "On the biology of the mite, *Glycyphagus domesticus* De Geer. (Tyroglyphidae, Acarina)." Ann. Appl. Biol. 21, 483–94.

An account of the life history, and of the effects of humidity and temperature on the life of the mite.

**36. MacLagen, S. (1933).** "The ecological significance of soil reaction (*p*H value) in relation to terrestrial animals." Proc. R. Phys. Soc. Edinburgh, 22, 107–22.

Previous work had shown that greatest earthworm and snail numbers are correlated with *p*H values of 6 to 7 and 7 to 8 respectively. Experiments with the springtail *Smynthurus viridis*, and counts in soils with different reactions, showed that the optimum *p*H value is about 6·3, and that values outside 6 to 7 inhibit growth, egg production, rate of egg-laying, and total population increase.

**37. Herford, G. V. B. (1934).** "An automatic humidity control." Ann. Appl. Biol. 21, 542–5.

An apparatus is described by means of which the humidity can be accurately controlled when the temperature is kept constant.

**38. Blackburn, K. B. (1934).** "Wasting disease of *Zostera marina*." Nature, 134, 738.

Chromosome studies proved that the narrow-leaved form of eelgrass have the same number of chromosomes as the normal form, and also *Z. nana*; but *nana* has much larger ones that are clearly distinguishable. Therefore the narrow-leaved form is not a hybrid: it is probably a phenotypic form living at a different level on the shore. The last conclusion is questioned by **C. Cottam**, Nature, 135, 306, 1935.

**39. Tutin, T. G. (1934).** "The fungus on *Zostera marina*." Nature, 134, 573.

*Ophiobolus halinus* was found at several places in Devon, on Guernsey, and Lough Ine in Ireland. It had already been found in North America (Atlantic coast) and in Denmark. It is absent from *Z. nana*, and may therefore be a possible cause of the recent disappearance of *Z. marina*.

### 4. PARASITES OF ANIMALS.

See also **10, 27, 32, 89, 90.**

**40. Thompson, G. B. (1934).** "The ectoparasites of British birds and mammals (an Appeal)." Scottish Nat. 173.

Lice, fleas, parasitic flies and beetles, bugs, ticks and mites wanted from any British mammal or bird or nests. These should be sent to G. B. T. at Dept. of Entomology, British Museum (Natural History), Cromwell Road, London, S.W. 7.

**41. Thompson, G. B. (1934).** "The parasites of British birds and mammals. II. Records of Ixodoidea (Ticks)." Ent. Mon. Mag. 70, 204–7.

Records of ticks from common shrew, polecat, jay, jackdaw, siskin, sand martin, mistle thrush, rock pigeon, little owl, sparrowhawk, shag, and cormorant.

**42. Cameron, T. W. M.** and **Parnell, I. W.** (1933). "The internal parasites of land mammals in Scotland." Proc. R. Phys. Soc. Edinburgh, 22, 133–5.

Specimens of most wild mammals except some of the smaller rodents were examined. The host records and localities are given for flatworms and roundworms.

**43. Elton, C. (1934).** "Metazoan parasites from mice in the Isle of Lewis, Outer Hebrides." Parasitology, 26, 107–11.

Wood-mice (*Apodemus hebridensis*), house mice (*Mus musculus*) and rats (*Epimys decumanus*) were examined: the fleas, mites, ticks and intestinal worms are recorded; also the fauna of some house mouse nests. The flea rate was low. This survey is the first of a series designed to throw light on the Quaternary history of the British Isles, through the study of island rodents and their parasites.

**44. Hora, A. M. (1934).** "Notes on mites collected from the Isle of Lewis, Outer Hebrides." Parasitology, 26, 361–5.

16 species of mites collected from *Apodemus hebridensis* and *Mus musculus*, and also from nests of the house mouse. Among others, a mite forming skin scabs on the legs of wood-mice (a species of *Notoedres*) and the tick *Ixodes tenuirostris*, are recorded. This collection formed part of the survey noted under **43**.

**45. Bishop, A. (1934).** "The intestinal Protozoa of a muskrat, *Fiber* (=*Ondatra*) *zibethica*, with a note on *Retortomonas* sp. from the guinea-pig." Parasitology, 26, 578–81.

Four species of flagellates from a muskrat caught in the River Severn, Shropshire. The only protozoan previously recorded from any muskrat was a coccidian.

**46. Hunter, S. A. (1934).** "Parasites of badger." Irish Nat. J. 5, 72.

A louse (*Trichodectes melis*) amd a flea (*Paraceras melis*) on a badger from Londonderry.

**47. MacLeod, J. (1934).** "*Ixodes ricinus* in relation to its physical environment: the influence of climate on development." Parasitology, 26, 282–305.

This sheep tick carries several diseases of domestic animals: red-water (piroplasmosis), louping ill, and tick-borne fever. The temperature and humidity conditions for development were studied experimentally. Larvae require a higher humidity (90–95 per cent.) and temperature (26–30° C.) for optimum development than the nymphs (85 per cent. and 22·5° C.). Under optimum physical conditions there seems to be a higher death-rate among nymphs than among larvae.

**48. Britten, H. (1933).** "*Ixodes ricinus* L. in North Lancashire." N. Western Nat. 8, 325.

The sheep tick was taken while sweeping grass and rushes on a hill near Coniston Lake.

**49. Ritchie, J. (1934).** "Sheep-maggot flies in Scotland." Scottish J. Agric. 17, 249–60.

This fly (*Lucilia sericata*) is spreading northwards, and by 1933 had reached Caithness. Of the Calypterate fly population on a typical pasture, 10 per cent. were *Lucilia*.

**50. Cram, E. B.** and **Wehr, E. F. (1934).** "The status of species of *Trichostrongylus* of birds." Parasitology, 26, 335–9.

The worm causing severe periodic epizootics among British grouse (*Lagopus scoticus*) has hitherto been described as *T. pergracilis*, while *T. tenuis* was the name used for a similar worm found in partridges (*Perdix perdix*) and other birds. These species have been re-examined and no constant differences found. They have therefore been combined into a new description of *T. tenuis*. No cross-infection has been demonstrated between partridge and grouse, so the possibility of specific strains or biological races is not precluded.

**51. Lowe, P. R. (1934).** "On a flock of razorbills in Middlesex found to be infested with intestinal flukes." British Birds, 28, 188–90.

15 razorbills picked up dead on Littleton Reservoir in October 1934, following a violent storm. All had inflamed recta with haemorrhage, and large numbers of flukes, *Cotylurus platycephalus*. These normally inhabit fish-eating birds and probably have an alternative freshwater host. It is thought that infection of the razorbills was accidental, as they also had three other worms whose larval habitat is probably in freshwater animals.

**52. Britten, H. (1934).** "A new British Chalcid bred from birds' nests." N. Western Nat. 8, 247–9.

*Bairamlia nidicola*, Ferrière, 1934, found in various birds' nests. It is probably a flea parasite.

**53. Aschner, M. (1934).** "Studies on the symbiosis of the body louse. 1: elimination of the symbionts by centrifugalisation of the eggs." Parasitology, 26, 309–14.

Lice die in six days when their symbionts are removed (by a technique that is described).

**54. Thompson, W. R. (1934).** "The Tachinid parasites of woodlice." Parasitology, 26, 378–448.

Full account of the larval structure of woodlouse (land Isopod) parasites. Four out of eight species studied were parasitised by Tachinid flies. *Porcellio scaber* and *Oniscus asellus* especially, probably because they live mainly under the bark of fallen trees. The parasite eggs are laid in crevices in bark, and the larvae wander from there on to the hosts. The ovaries of parasitised females are reduced owing to the parasites eating part of the fat supply.

**55. MacGill, E. L. (1934).** "On the biology of *Anagrus atomus* (L.) Hal.: an egg parasite of the leaf-hopper, *Erythroneura pallidifrons*, Edw." Parasitology, 26, 57–63.

Describes life history. The leaf-hopper was living on *Primula* leaves, and parasites were found in Cheshire in 1930 and 1932.

**56. Lal, K. B. (1934).** "Insect parasites of Psyllidae." Parasitology, 26, 325–34.

Psyllid (bug) apple pests in Scotland are parasitised by six Hymenopterous and one Dipterous parasite. There are one or two hyper-parasites. (A new species of Cecidomyid fly parasite is described.) A table of the known world distribution of Psyllid parasites is given.

**57. Jackson, D. J. (1934).** "Notes on parasites of *Abraxas grossulariata* in Fife." Scottish Nat. 143.

The magpie was found to be parasitised in the caterpillar stage by Tachinid flies (*Phryxe nemea*) and Braconids (*Apanteles limbatus*), and in the pupal stage by Ichneumonids (*Pimpla examinator* and *Stenichneumon trilineatus*). The last had a hyperparasite, the Pteromalid *Habrocytus morenes*.

**58. Robertson, D. (1935).** "The stem eelworm disease of oats and its control." Scottish J. Agric. 18, 47–52.

Refers to *Anguillulina dipsaci*. Soil samples taken a week after the oat harvest showed over eleven hundred million worms per acre.

**59. Chrenko, F. A. (1934).** "A list of parasitic Rhabdocoela (Turbellaria) of Plymouth." Parasitology, 26, 114–16.

Flatworms from Echinoderms, the Crustacean *Nebalia*, and from the cockle (*Cardium*).

**60. Boxhall, G. N., Happold, F. C.** and **Lloyd, Ll. (1934).** "Quinanil as a bactericidal agent in the isolation of an insect flagellate." Parasitology, 26, 44–8.

Used successfully to kill contaminating bacteria in cultures of flagellates from the Anthomyiid fly *Polietes*.

**61. Burnet, F. M. (1934).** "The bacteriophages." Biol. Rev. 9, 332–50.

Bacteriophages have many properties in common with filterable viruses, but the former live in association with growing bacteria, and the latter with living animals or higher plants. They are both parasitic or symbiotic. They are both within the same range of size: the smallest bacteriophage is the same size as the smallest known virus, that of foot and mouth disease, which is probably 8–12 $m\mu$. They are both unable to grow away from living material. Bacteriophages may be confined to one or more species. They are often constant over widely separated areas. Some dysentery bacteriophage types are the same in India, Australia and England. In their natural habitats phages do not wipe out the host culture bacterial population, but this may happen in cultures.

5. FOOD AND FOOD-HABITS.

See also **8, 13, 24, 79, 81, 82, 83, 86.**

**62. Clowes, E. F. (1933).** "Stoat feeding young on rock pipits." Irish Nat. J. 4, 217–8.

**63. Hay, I. (1934).** "Feeding of common terns." Scottish Nat. 136.

Terns were nesting in Balgray reservoir (inland near Glasgow) but bringing fish from the White Cart River some way off to feed their young.

**64. Thomas, J. F. (1934).** "The food of nestling swallows." British Birds, 28, 171–2.

Samples taken from the beaks of swallows going to feed young in Carmarthenshire contained 12 genera of flies, 2 of beetles, 1 moth, 1 bug, and 1 Pimpline Hymenopteron.

**65. Brindley, M. D. (1934).** "Swallows capturing butterflies on the wing and feeding their young on Lepidoptera; Pentatomid bugs swallowed by coots." Proc. R. Ent. Soc. Lond. 9, 68.

Further references to the attacks of birds on insects by **M. D. Brindley,** *ibid.* 69; **E. B. Poulton,** *ibid.* 70–1; **G. D. H. Carpenter,** *ibid.* 47–8; **J. G. Myers,** *ibid.* 58.

**66. Jones, F. M. and others (1934).** "Replies to Dr W. L. McAtee's rejoinder in Proc. R. Ent. Soc. Lond. 8, 113–26, to papers on protective adaptations published by the Society (loc. cit. 7, 79–105)." Proc. R. Ent. Soc. Lond. 9, 21–40.

Eleven authors continue the discussion on Dr McAtee's belief (based upon an examination of the food-contents of 80,000 birds' stomachs) that availability is the chief factor involved in the choice of food of birds and that the phenomena classed by theorists as protective adaptations have little or no effectiveness. All unite in criticizing McAtee's methods and conclusions. **R. A. Fisher** (p. 26) states that McAtee claimed to show that availability was so important that protective adaptations could not be effective whereas he had only shown that abundance was an important factor. From this fact was drawn the illegitimate inference that other factors must be unimportant. **H. B. Cott** (p. 31–5) brings forward evidence that more Hymenoptera were found in the stomachs of British toads than in the stomachs of frogs, and that bees are unpalatable to toads, who quickly learn to avoid them.

**67. Hobby, B. M. (1934).** "Predacious Diptera and their prey." J. Soc. British Ent. 1, 35–9.

New records of the prey of robber-flies, dung-flies and of the Anthomyiid, *Coenosia tigrina*.

**68. Hobby, B. M. (1934).** "Notes on predacious Anthomyiidae and Cordyluridae (Dipt.)." Ent. Mon. Mag. 70, 185–90.

Predacious flies.

**69. Hobby, B. M. (1934).** "The prey of dragonflies." Ent. Mon. Mag. 70, 191–2.

Two new records additional to previous lists (**H. G. Attlee,** Entomologist, 66, 100–3; 67, 158–62, and **B. M. Hobby,** Trans. Ent. Soc. S. Eng. 8, 65–76; J. Ent. Soc. S. Eng. 1, 106). *Pyrrhosoma nymphula* with *Plemyria sociata*, and *Agrion puella* with an immature Cercopid bug.

**70. Burkill, H. J. (1934).** "Food-plant of *Chaerocampa elpenor* Linn." Entomologist, 67, 227.

*Menyanthes trifoliata* recorded as a food-plant. Further reference by **C. Nicholson,** *ibid.* 236 (eggs on *Gentiana sino-ornata*).

**71. Poulton, E. B. (1934).** "Attacks of common wasps upon butterflies: wasp carrying off spider's prey." Proc. R. Ent. Soc. Lond. 9, 71–2.

**72. Goffe, E. R. (1934).** "*Empis livida* Linn. (Dipt., Empid.) as a factor in the control of *Tortrix viridana* Linn. (Lep., Tortr.)." J. Soc. British Ent. 1, 45–6.

Males of *Empis livida* were observed preying in large numbers upon the green oak *Tortrix* in Hampshire in June, 1934. Both fly and moth were abundant at the time. The males are well-known to capture prey for presentation to the females during courtship.

**73. Mansour, K.** and **Mansour-Bek, J. J. (1934).** "The digestion of wood by insects and the supposed rôle of micro-organisms." Biol. Rev. 9, 363–82.

A review of the literature shows that there is no valid evidence that termites really depend on the activity of intestinal protozoa for breaking down cellulose into digestible food. One of the most important termites economically has no intestinal Protozoa. It is suggested that the presence of cellulase, an enzyme occurring widely among wood-eating insects (some beetles and their larvae, and termites), may be the real agent in promoting digestion of wood.

## 6. ANIMAL POPULATIONS.

See also **13, 36, 50, 51.**

**74. Matheson, C. (1933).** "Notes on domestic and wild animals in Montgomeryshire." In "Collections Historical and Archaeological relating to Montgomeryshire and its Borders", pp. 75–95. (Welshpool, David Rowlands Ltd.)

A very interesting review of the changes in status of Welsh animals and birds. It deals with sheep (it is suggested that a Roman breed survived on Ramsey Island, Pembrokeshire, until recent historic times); cattle (there is a discussion of the Neolithic oxen races); horses (derived from an indigenous hill race crossed with Spanish horses); pigs (which were much more like wild boars a hundred years ago); various birds and animals of prey, including wolf (extinct by the sixteenth century), bear (extinct before the tenth century), wild cat (extinct recently), golden eagle (occurring in Snowdonia until the end of the eighteenth century); red deer (formerly abundant, but extinct by about the end of the eighteenth century); rats; rabbit (probably introduced about Norman times but not spreading widely until the nineteenth century); pheasant; little owl; and muskrat.

**75. Fisher, N. (1934).** "The last Irish wolf." Irish Nat. J. 5, 41.

Killed about 1786 in Co. Carlow.

**76. Munro, T. (1935).** "Notes on musk-rats and other animals killed since the inception of the campaign against musk-rats in October 1932." Scottish Nat. 11–16.

During two years 945 muskrats were trapped in Scotland, mostly in traps set in shallow water. Other mammals, and birds, caught accidentally in the traps included 2305 water voles, 1745 common rats, 2178 moorhens, 101 ducks, 18 herons, and representatives of most of the other species that haunt water margins. There was a rather unexpectedly large proportion of stoats and weasels caught (36 and 57 respectively).

**77. Anon. (1934).** "Musk-rats in Scotland." Scottish J. Agric. 17, 94–8.

5 females and 4 males escaped from a farm started in 1927 near Feddal, Perthshire. 890 had been killed by trapping campaigns up to the end of 1933. Notes on habits and methods of trapping.

**78. Emmet, H. J. (1934).** "Swallow clutches and broods." British Birds, 28, 146.

At one place in Sussex, the average clutch of 7 nests was 4·4, the average number of young fledged 2·9. Of 31 eggs layed, 84 per cent. hatched and 65 per cent. fledged.

**79. Mayall, A. (1934).** "Number and destruction of broods of nightingales in Suffolk." British Birds, 28, 145–6.

Nightingales, abundant in 1934, had many nests destroyed (over 25 out of 70) probably by rats and mice (eating eggs) and stoats (destroying parents or young).

**80. Beveridge, G. (1934).** "Increasing birds in North Uist." Scottish Nat. 169.

Increase of starling, corncrake, eider duck, lesser tern, and dunlin.

**81. Anon. (1935).** "Starlings in London." Nature, 18.

Editorial quotes the Report for 1933 of the Committee on Bird Sanctuaries in Royal Parks (England). **C. S. Baynes** reports that starling roosts on Duck Island in St James's Park continued throughout the summer with several thousand birds. This is unusual. **R. W. Hale** traced the feeding ground of some of the huge flocks that roost on Central London buildings in winter to the Hendon Sewage Farm.

**82. Pollard, R. S. (1934).** "Bird life on the Saltees." Irish Nat. J. 5, 30–33.

Notes on the changes in numbers on these islands since 1929. Increase in herring gulls and greater black-backed gulls (latter causing decrease in puffins); fluctuations in cormorants; a few fulmar petrels and gannets. Additional comments by **T. H. Mason**, Irish Nat. J. 5, 71–2: Manx shearwaters were abundant in 1911.

**83. Ryves, Mr and Mrs B. H. (1934).** "Supplementary notes on the breeding-habits of the corn-bunting, as observed in North Cornwall in 1934." British Birds, 28, 154–64.

Polygamy is widespread in this species, in one instance a single male being found owning seven females. 53 nests were found and watched. Of these 13 lost the chicks (desertion, human destruction, weasel, and ? adders). 144 young were fledged from 40 nests. The food this year was somewhat different from before, perhaps owing to scarcity of cabbage white caterpillars. It included grasshoppers. There are nesting territories, but no feeding territories.

**84. Robinson, H. W. (1934).** "Mortality among young common terns in Lancashire." British Birds, 28, 211–12.

Mortality (proved by ringing young) was 4 per cent. in 1929 (very hot), 5 per cent. in 1930 (very hot), 3 per cent. in 1931 (cold and wet), 5–6 per cent. in 1932 (hot), 12 per cent. in 1933 (hot and dry, also some shot), 8 per cent. in 1934 (hot and dry). Mortality attributed to visitors keeping parents from sheltering young from hot sun.

**85. Huxley, J. S. and Best, A. T. (1934).** "A census of water-birds on the Highgate and Kenwood ponds." British Birds, 28, 122–9.

Mute swan, mallard, pochard, tufted duck, coot, moorhen, dabchick, blackheaded and common gulls, distributed over a series of nine ponds, varied greatly in numbers from week to week, between January and June. Gulls, abundant till February, decreased and left in March and April. Swans mostly stayed to breed, showing little territorial hostility. Pochard left by March, and tufted duck by May, without breeding. Mallard remained to breed. The fluctuating sex-ratios in ducks indicated much movement from March onwards. High mortality among young mallards and moorhens. Coots and moorhens decreased by the spring, but many bred, though rather late, and had strong territory reactions.

**86. Venables, L. S. V. and Lack, D. (1934).** "Territory in the great crested grebe." British Birds, 28, 191–8.

Three years' observations on two ponds on the Surrey-Hampshire border. High mortality among eggs (due to collectors) and young (due to hungry pike). In 1932 and 1933 the average number of young successfully reared by each pair was 1·5, while under greater protection in 1934 it was 2·5. Observations suggest that territory size varies in different pairs and that this is connected with different temperaments and not at all with food supply.

**87. Nall, G. H. (1934).** "Sea trout of Lewis and Harris." Fishery Board for Scotland, Salmon Fisheries 1934, No. 4, pp. 1–71. (H.M. Stationery Office, Edinburgh or London. 4*s*., postage extra.)

Contains a summary description of the lochs. Notes that salmon have increased in numbers and size in recent years, although sea-trout have somewhat decreased. Gives a detailed analysis of scale readings and conclusions to be drawn from them.

**88. Welch, R. J. (1934).** "Revival of an old escallop fishery." Irish Nat. J. 5, 41–2.

Revival of fishing for *Pecten maximus* in Co. Down. This was formerly a locally important industry.

**89. Rosenberg, H. T. (1934).** "A study of the colonisation of *Aphelinus mali* Hald." Trans. R. Ent. Soc. Lond. 82, 415–20.

An account of the successful use of a Chalcid (Hymenopteron) in controlling woolly aphis by parasitization, with details of the rate of spread of the parasite in orchards and suggestions for its practical use as a control.

**90. Thompson, W. R. (1934).** "The development of a colony of *Aphelinus mali*, Hald." Parasitology, 26, 449–53.

A census taken in early June 1933 of a woolly aphis colony (*Eriosoma langigerum*) at Farnham Royal, Buckinghamshire, gave a figure of 112,000. 300 *Aphelinus* were introduced in mid-June. The parasites practically annihilated the aphis colony within 64 days.

**91. Donisthorpe, H. (1934).** "Abundance of *Melolontha vulgaris*, Fb., in Windsor Forest." Ent. Rec. 46, 94.

In May 1934 the common cockchafer occurred in large numbers in the Windsor Forest area where normally only a few specimens are seen.

**92. Tulloch, J. B. G. (1934).** "Swarm of *Melolontha vulgaris* in Monmouth." Entomologist, 67, 260.

The swarming of this cockchafer lasted for about ten days, starting from May 12th.

**93. Richards, O. W. (1934).** "The number of generations of *Pieris rapae* L. in Southern England." Proc. R. Ent. Soc. Lond. 9, 78–9.

Observations made on the number of eggs present on a certain row of cabbages, showed that there are three distinct non-overlapping oviposition periods indicative of three broods.

### 7. MIGRATION, DISPERSAL, AND INTRODUCTIONS.

**94. Elder, H. F. D. (1935).** "Isle of May Bird Observatory." Scottish Nat. 1–2.

The Midlothian Ornithological Club has set up a station for watching migrants and ringing them, on the Isle of May in the Firth of Forth. Funds are needed (J. H. B. Munro, 20 Murchison Gardens, Edinburgh), also volunteers to work on the island.

**95. Witherby, H. F. and Leach, E. P. (1934).** "Movements of ringed birds from abroad to the British Isles, and from the British Isles abroad." British Birds, 28, 106–12, 133–41.

Deals with a number of species. There are maps for the starling, and blackbird, showing the east and west movement; for cuckoo, showing it wintering in North Italy, Central Europe and West Africa; and for the heron, which shows both types of movement. Unusual numbers of lapwings wintered in France and Spain in 1933–4.

**96. Witherby, H. F. and Leach, E. P. (1934).** "Emigration of Lapwings in winter." British Birds, 28, 208–9.

Clifton College Scientific Society noted that lapwings disappeared from large areas of Somerset, Hampshire and Dorset in December. A keeper in Hampshire saw large flocks flying out to sea, together with wood pigeons (see No. **95**).

**97. Marples, S. (1933).** "Homing tits and other birds." N. Western Nat. 8, 199–200.

Experiments in which birds were taken away, and succeeded in homing several miles, often within a comparatively short time.

**98. Duncan, J. C. (1933).** "Grass snakes released in Co. Longford." Irish Nat. J. 4, 199.

Three snakes released about 1928 were killed in 1931, 1932, and 1933. No evidence that they had bred. Several previous introductions round Dublin were also unsuccessful.

**99. Stephen, A. C. (1934).** "Long-finned tunny (*Thynnus germo*) in the Holy Loch, Argyll." Scottish Nat. 128.

The third record of this Mediterranean fish in Scottish waters.

**100. Stephen, A. C. (1934).** "John dory (*Zeus faber*) in Glenelg Bay, Inverness-shire." Scottish Nat. 164.

Taken in June 1934.

**101. Parkin, E. A. (1934).** "The occurrence of the longhorn beetle, *Hylotrupes bajulus*, L., in England." Forestry, 8, 150–4.

This species occurs normally in open country. Recent cases of it damaging softwood timber in houses may be due to importation in timber from the Baltic, where it is a common pest.

**102. Staniland, L. N. (1934).** "The loganberry cane maggot." J. Minist. Agric. 41, 151–3.

This Anthomyid fly (*Phorbia? pudica*) appeared in South Devonshire in 1933, possibly introduced from America.

**103. Williams, C. B. (1935).** "Immigration of insects into the British Isles." Nature, 135, 9–10.

A useful summary of recent work on immigrant insects, especially Lepidoptera, which include some 12 butterflies (nearly 20 per cent. of our British species), about half the British hawk moths, as well as a number of other moths. Some (clouded yellow, painted lady, etc.) come from the South of Europe or even North Africa, others (cabbage white) from the Baltic area, or (Camberwell beauty) from Scandinavia; while the milkweed butterfly comes from America. Most of the hawk-moths come from the south. There are a dozen dragonfly immigrants, some fairly common visitors. There is now some evidence that the red admiral, at least, has a return flight south in autumn. The means by which flight direction is kept is still a mystery: it is not explained by winds. The South-Eastern Union of Scientific Societies has a permanent Insect Immigration Committee under Capt. T. Dannreuther, which has a widespread organization of observers. The co-operation of lighthouse and light-ship keepers has also been recently obtained.

**104. Dannreuther, T. (1934).** "*Danaus plexippus* L." Entomologist, 67, 164.

Additional records bring the total number of independent observations in 1933 to thirty, which is the largest number ever seen in one year in the British Isles. Further references by **T. Dannreuther**, *ibid.* 209; and in Ent. Mon. Mag. 70, 180–1.

**105. Dannreuther, T. (1934).** "Migration records." Entomologist, 67, 186–90.

The first hundred records sent in for 1934 indicate that the spring insect immigration of Lepidoptera was on a smaller scale than in 1933. Further references by **T. Dannreuther**, *ibid.* 211–15, 239–40, 254–7, 279.

**106. Maxwell, H. (1934).** "The peacock butterfly (*Vanessa io*)." Scottish Nat. 173–4.

About 30 specimens grown from pupae were released at Monreith, Wigtownshire, in 1931. None seen until 1933 (one specimen, seven miles away). In 1934 seven were seen up to 30 miles away.

**107. Workman, W. H. (1935).** "The peacock butterfly." Scottish Nat. 22.

Records a few in Northern Ireland in 1933, but extremely large numbers in 1934. It is thus likely that Maxwell's records (see No. **106**) were part of a general increase or spread, and not the progeny of his liberated specimens.